PATTERSON, THOMAS WILLIAM, Ph.D. Longleaf Pine Masting, Climate Variability, and Tick-Borne Disease Prevalence in the Southeastern U.S. (2017)
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This dissertation consists of three manuscripts that have been prepared for or accepted by peer-reviewed academic journals. I first examined the relationship between longleaf pine (*Pinus palustris* Mill.) mast (i.e., cone crop) and radial growth at three locations in North and South Carolina. In this chapter I showed how the reduction of stand density improved annual mast but neutralized mast/ring-width relationships. I then examined the relationship between mast and radial growth at four additional locations (six sites) in more detail. I compared tree-level mast and radial growth data to determine how mast crops of varying sizes influenced radial growth, and how mast data could be integrated with radial growth chronologies when examining relationships with climatological data. Only the largest mast crops significantly modulated radial growth and these data were a minor contribution to regression-based analyses of radial growth and climate. Finally, I explored the relationship between longleaf pine mast and tick-borne diseases throughout the southeastern U.S. Disease ecologists have linked masting cycles of hardwood tree species (e.g. Oak) to tick-borne diseases such as Lyme, yet no research has extensively studied the influence of southeastern U.S. pine mast on diseases of the region. I used correlative analyses that showed the relationship between mast and three tick-borne diseases in humans that were linked via the consumptive behavior of Northern Bobwhite Quail (*Colinus virginianus*).

LONGLEAF PINE MASTING, CLIMATE VARIABILITY, AND TICK-BORNE DISEASE PREVALENCE IN THE SOUTHEASTERN U.S.

by

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CHAPTER I

INTRODUCTION

1.1 Background on Longleaf Pine

Longleaf pine (*Pinus palustris* Mill.) is a long-lived (i.e. > 400 years, Earle, 2017) species native to the southeastern US (Figure 1.1). Stands of longleaf occur principally along the Coastal Plain and lower Piedmont physiographic regions, but outlier montane stands exist in the Ridge and Valley regions of Alabama and Georgia and the Uwharrie Mountains of central North Carolina (Patterson and Knapp 2016a). The species' range has diminished from an estimated pre-settlement coverage of 37 million hectares (Frost 1993) to 1.74 million hectares (Oswalt *et al.* 2012) due to various anthropogenic processes. Longleaf pine forests have adapted to highly disturbed landscapes that include frequent surface fires and damaging tropical-storm winds (Brockway *et al.* 2006). Due to fire suppression, logging without reforestation, and land-use changes that have reduced the longleaf pine range (Frost 2006), research targeted at better understanding climate/growth/mast interactions in this diminishing ecosystem may contribute to ongoing restoration strategies (Brockway *et al.* 2006).

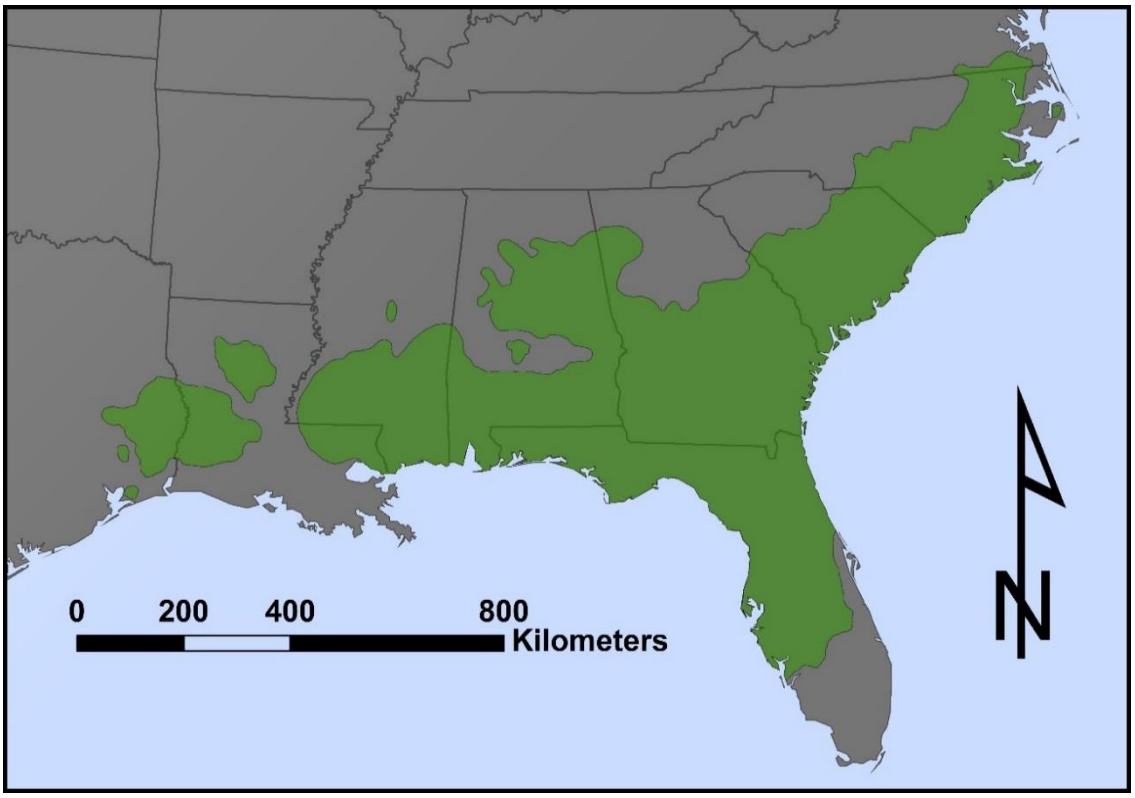

Figure 1.1. Map Of The Prehistoric Extent Of Longleaf Pine.

Early accounts of longleaf pine forests describe vast expanses of pine-savannah grasslands that blanket the southeastern U.S. This perception, as vividly described by Bartram (1791), created a perception that longleaf pine savannahs were the dominant longleaf pine ecosystem through much of its range. Currently, however, there is a better understanding about the diversity of ecosystems that are associated with longleaf pine. Over one hundred unique vegetation classes are associated with longleaf pine forests and much of this variation is attributed to subtle changes in environmental conditions from the xeric, sandy coastal plain to the southern Appalachian mountain region (Peet 2006). Subtle variations of only a few centimeters elevation, particularly in the coastal plain, can create radically different ecotones where numerous plant and animal species can live. Recently the

longleaf pine range has been encapsulated within the North American Coastal Plain Floristic Province as the 36th global biodiversity hotspot (Noss *et al.* 2015). Here, floral species exceed 6,000 with over 1,800 endemic to the coastal plain (Noss *et al.* 2015). Most suitable habitat for longleaf pine has been removed through anthropogenic processes and natural fire regimes have been all but eliminated (Peet 2006). As a result, restoration strategies are inherently difficult due to a discontinuous range that spans a continuum of environmental conditions harboring unique species with special considerations and habitat needs.

Longleaf pine radial growth is positively influenced by precipitation throughout its range, whereas the effects of temperature are site specific. Warm-season precipitation is the most influential climate factor on radial growth (Knapp *et al.* 2016; Henderson and Grissino-Mayer 2009; Lodewick 1930; Devall *et al.* 1991), followed by cool-season precipitation in northern stands (Bhuta *et al.* 2009). Coile (1936) was the first to identify a negative relationship between radial growth and temperature, later confirmed by Henderson and Grissino-Mayer (2009). Lodewick (1930) failed to detect a relationship to temperature, whereas Bhuta *et al.* (2009) found a positive relationship to winter temperatures. Patterson *et al.* (2016) documented stronger summertime climate responses for lower Piedmont stands compared to coastal plain populations in North Carolina.

1.2 Longleaf Pine Cone Development

Longleaf pine trees are monoecious whereby each tree has male strobili or catkins (Figure 1.2a) in the lower crown and female strobili conelets (Figure 1.2) in the upper crown (Schopmeyer 1974).

Figure 1.2. Male Catkins (Left) And Female Conelets (Right) Of Longleaf Pine. Images Adapted From Forestryimages.org

Catkin development typically begins during July and conelet development follows shortly after in August (Boyer 1990). Shoulders (1967) determined catkin production flourished with abundant growing-season rainfall, whereas conelet production is initiated by a wet spring followed by a dry summer. Boyer (1990) noted that due to this preferential difference to developmental conditions, large strobili crops rarely coincide. Development continues through the winter months until pollination the following spring (Boyer 1990), occurring as soon as late February in the southern range to early April at its northern extent (Boyer 1990) and lasting for 5–21 days.

Annual variations in the onset of pollen shedding are temperature dependent and related to cumulative warm days ($> 10^0$ C) after January 1st (Boyer 1972; Boyer and Woods 1973). Conelet losses can range from 60–100% (Boyer 1974) due to weather extremes, frosts, insects, and insufficient pollination (Brockway *et al.* 2006). Longleaf pine conelets remained pollinated for 12 months until fertilization occurs the following spring (Brockway *et al.* 2006). Cone production begins the spring following pollination, with cone growth

ranging 10–25 cm by early summer and changing color from green to brown as they ripen (Schopmeyer 1974). The seeds within the cones are wind dispersed during a 2–3 week period during late October and early November (Brockway *et al.* 2006). Longleaf pine have the largest seeds of the southern pines, and 71% of seeds fall within 20 meters of the parent tree (Croker and Boyer 1975). The number of seeds per cone ranges from 50 seeds/cone during favorable years, 35 seeds/cone during average years, and as few as 15 seeds/cone during poor years (Croker 1973).

1.3 Longleaf Pine Cone Production

Early literature on longleaf pine cone crops (i.e. mast) is anecdotal (Boyer 1998). Wahlenberg (1946) notes good cone crops occur every 5–7 years, with heavy ("bumper") cone crops occurring over much of the species' range once every 8–10 years (Maki 1952). To enhance reforestation strategies, Dr. William Boyer of the USFS began recording annual cone crop at multiple sites starting in the late 1950s to mid-1960s; a practice continued today under the direction of Dr. Dale Brockway. For longleaf pine to naturally regenerate, Boyer (1993, 1997) states a minimum of 750-1000 cones per acre (40–75 cones per tree depending on stocking) are required. As cone production varies both spatially and annually (Boyer 1987), adequate cone production for less dense stands (75 cones per tree, 10 trees per acre) may occur once every 30–40 years, and every 8–10 years for more dense stands (25–30 trees per acre) (Boyer 1997). Peak cone production is reached in well stocked, uneven aged stands that produce adequate cone crops every 4–5 years (Croker and Boyer 1975), and can be improved by reducing stand densities to between 6.9–9.2 m^2 per hectare (Boyer 1979). The official USFS rating system categorizes longleaf pine cone crops by reporting the average

cones per tree from failed (< 10) to bumper (≥ 100) with three intervals in-between (poor (10–24), fair (25–49), good (50–99)).

Due to the difficulties with natural regeneration of longleaf pine Dr. Boyer began tracking cone production of longleaf pine trees at select sites in the Escambia Experimental Forest in southern Alabama in the late 1950s. Since then, the number of sites has fluctuated from eleven to fourteen at uneven-aged shelterwood sites throughout the range of longleaf pine as part of a multidecadal study titled the "Longleaf Regeneration Trials" (Connor *et al.* 2014). Presently, Dr. Brockway oversees data collection and reports site averages annually. At each stand the number of green cones and conelets are counted for at least 10 trees each spring using binoculars (Brockway 2016). Individually numbered trees are resampled annually, and averages are compiled from the individual, mature cone-baring trees in each reporting station. Results of these cone counts are published each summer and are disseminated to foresters throughout the Southeast to alert when favorable cone crops are expected that autumn. In the 2015 cone report, Dr. Brockway noted "News of a good cone crop usually alerts forest managers to get busy during the summer, preparing seedbeds that will be receptive to capturing and deriving the most benefit from the upcoming seed shed" (Brockway (2015).

Improvements in average cone production have been witnessed throughout the longleaf pine range from 14 cones per tree/year during 1966–1985 to 36 cones per tree/year during 1986–1995 and this has been attributed to improvements in flower production (Boyer 1998). Individual tree cone production is influenced principally by genetics however tree size, crown class, stand density, and site quality are also important (Brockway *et al.* 2006).

Open-grown, large-crown longleaf pine produce the greatest number of cones in a site (Croker and Boyer 1975), and trees of 38–48 cm diameter at breast height (DBH) produce on average 65 cones/year whereas trees 25–33 cm DBH produce 15 cones per year (Boyer 1990). Natural regeneration of longleaf pine is hampered by a suite of conditions including insufficient number of cone-producing trees, infrequent cone crops, cone infestations by insects, fungi, and/or seed predation, limited cone dispersal distance, lack of mineral soil, slow-early growth, untimely fires, and fire exclusion that favors competing species (Brockway *et al.* 2006). Boyer (1997) underscores the importance of monitoring and tracking cone crops to appropriately forecast years when good crops are available (i.e. masting years).

1.4 Masting Ecology

Mast is a general botany term used to identify the fruits of forest trees such as acorns and nuts. The term comes from the Old English word, *mæst*, meaning accumulated nuts on the forest floor used as forage to fatten swine (Koenig and Knops 2005). Many of the masting tree species produce episodic and synchronous, large annual yields known as masting years/events (Kelly 1994; Koenig and Knops 2005). During masting years, a population of masting tree species will produce an abundance of fruits, sometimes over a geographic range of hundreds of miles, yet reasons for this phenomenon are complex and not fully understood (Kelly and Sork 2002). Non-masting years are identified as the intervening years when masting species produce little or no fruit (Silvertown 1980). Masting research is diverse and includes studies that seek to explain drivers for masting events (Isagi *et al.* 1997) and its effect on the ecology of tick-borne diseases such as Lyme disease (Levi *et al.* 2012; Ostfeld 1997). Most tick-borne disease incidences vary annually (Gubler *et al.* 2001)

and studies (Ostfeld *et al.* 2006; Jones *et al.* 1998; Ostfeld *et al.* 2001) consistently identify mast quantity as an influence on tick-borne disease prevalence (Figure 1.3).

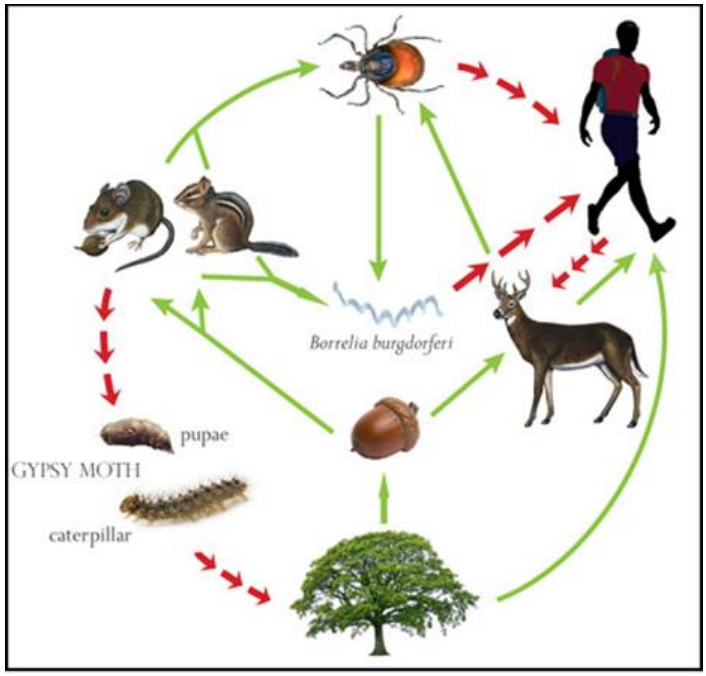

Figure 1.3. The Lyme Disease Web For Hardwood Species. Source: The Carey Institute.

Several theories exist that explain masting as an adaptive feature that includes resource tracking (Koenig and Knops 2005), predator satiation (Janzen 1971; Ims 1990; Silvertown 1980), increased wind-dispersal efficiency (Smith *et al.* 1990; Mooney *et al.* 2011), and seed-dispersal attraction (Christensen and Whitham 1991). Resource-tracking theory (Kelly 1994) states that trees produce annual mast in response to direct resources available to that tree such as favorable climatic conditions. This theory is not fully supported since variation in rainfall and temperature do not coincide with the magnitude of variation in mast. Similarly, tree species trade-off growth during masting years producing narrow growth rings (Speer 2001; Koenig and Knops 2005). Predator satiation theory states that large seed crops

are more effective at escaping near-complete consumption than smaller crop years (Koenig and Knops 2005), and may be the primary driver of masting in North American oak forests (Kelly and Sork 2002). Wind dispersal theory asserts that trees increase their chances of pollination if done synchronously. Similarly, if a large number of seeds are produced at once the likeliness of dispersal also improves (Christensen and Whitham 1991).

Kelly *et al.* (2008) summarized and compared mast seeding communities in North America with those in New Zealand to understand the differences in long-term masting events. They concluded that North American deciduous oak forests were more complex and less resistant than similar forests in New Zealand. Additionally, Kelly *et al.* (2008) suggest a better understanding of the different system responses of masting events, such as in influence of masting on predator and parasite populations, that would lead to a richer understanding of the ecosystem functions as a whole.

1.5 Masting and Tree Rings

Masting research is limited to annual yield data of masting species, thus the need to create accurate, long-term records for analysis. Szabó (2012) identified over eight centuries of archival information regarding European masting species, and concluded that accuracy and availability were highly variable. It is assumed that during large mast years trees drain internal carbon stores (Kozlowski and Pallardy 1997). As trees trade-off resources (i.e., carbon) from radial growth to reproduction, linkages can be made between the volume of mast and annual radial growth. Early studies (Holmsgaard 1958; Eis *et al.* 1965) have identified the negative influence of mast crop on radial growth. More recently, others (Speer (Drobyshev *et al.* 2014, Hacket-Pain 2015) have developed methods to analyze mast and

growth rings. Speer (2001) provided evidence for the potential to reconstruct acorn yield from five oak species from 17 sites in the southern Appalachian Mountains. Speer's successful reconstruction of acorn masting combined USFS acorn data with chronologies from 845 trees to reconstruct annual acorn yield. Additionally Speer (2001) found a significant, positive correlation ($r = 0.34$; $p < 0.1$) between acorn mast lagged three years and black bear population. Drobyshev *et al.* (2014) developed a 253-year long European beech (*Fagus sylvatica*) masting record from three sites in southern Sweden. The authors identified climatic drivers that influenced masting years that included a cool summer two years prior to masting followed by a warm summer one year prior to masting. Additionally, Drobyshev *et al.* (2014) tested whether the increase in European beech masting frequency in the latter half of the 20th century was significantly higher than periods throughout the 253-year reconstruction, but found no significant differences. Hacket-Pain *et al.* (2015) joined mast with climate data to explain more variance in growth rings. At present, no research has examined the influence of annual mast on longleaf pine growth rings.

1.6 Tick-Borne Disease Ecology

Ticks transmit a host of pathogens that are zoonotic in nature, meaning they have the capacity to facilitate the exchange of bacterial diseases between humans and various animal species (Pfäffle *et al.* 2013). Both the number of identifiable tick-borne diseases and pathogens have increased since the mid-1980s (Paddock and Telford 2011), largely driven by interest in Lyme disease (Bacon *et al.* 2008). Studies concerning tick-borne diseases have been principally conducted in the Northeast US due to the presence of Lyme (Ostfeld 1997), but an array of tick species harboring similar diseases with known public impacts are of

growing concern in the Southeast (Stromdahl and Hickling 2012). The Gulf Coast Tick (*Amblyomma maculatum* Koch), whose range closely resembles that of longleaf pine, is the principal carrier of the bacteria *Rickettsia rickettsia* and agent of concern for Rocky Mountain Spotted Fever (Paddock and Goddard 2015; Parola *et al.* 2013). Other southeastern U.S. species included the Lonestar Tick (*Amblyomma americanum*), the American Dog Tick (*Dermacentor variabilis*), Brown Dog Tick *(Rhipicephalus sanguineus),* and the Blacklegged Tick *(Ixodes scapularis).* These species are known to transmit a suite of bacteria that collectively make up the spotted fever group *rickettsiae* (SFGR), *Ehrlichia chaffeensis,* as well as Lyme disease (Childs and Paddock 2003; Stromdahl and Hickling 2012; Nadolny *et al.* 2014). Tick abundance is positively associated with deer abundance, with the white-tailed deer (*Odocoleus virginianus*) serving as a host vector that has significantly grown in population during the last century (Paddock and Yabsley 2007; Pichon *et al.* 1999; Pfäffle *et al.* 2013). As the risk for tick-borne diseases increases throughout the Southeast (Stromdahl and Hickling 2012), methods such as prescribed burning have displayed promise toward reducing tick populations (Hoch *et al.* 1972; Mather *et al.* 1993; Gleim *et al.* 2014). Specific to longleaf pine forests, and with field sites at the J.W. Jones Ecological Research Center, Gleim *et al.* (2014) found a significant reduction in four species of ticks associated with long-term prescribed burning that they deem consistent with previous research regarding the influence of fire in pine and mixed-pine forests (Jacobson and Hurst 1979; Cully 1999). At present, no one has investigated whether longleaf pine mast is related to tick-borne illnesses throughout the southeastern U.S.

1.7 Dissertation Objectives

This dissertation examines the relationship between longleaf pine cones and radial growth, and how longleaf pine cones relate to tick-borne diseases throughout the southeastern U.S. Chapter two examines mast/radial-growth relationships at two locations in North and South Carolina. Here, mast data were acquired at the stand level (average mast) and compared to radial-growth chronologies. I examined how the influence of selective logging improved annual mast and neutralized mast/radial-growth relationships. Chapter three examines mast/radial-growth relationships at six sites in four locations in Alabama, Florida, and Georgia using different techniques. At these sites, I gained accessed to individual-tree mast data and was permitted to sample from the actual trees used in the multi-decadal cone count study. I examined how mast quantities arranged by class (failed–bumper) influenced radial growth rings, and tested whether mast is a useful predictor of climate data when paired with radial growth using liner regression. Chapter four explores the relationship between longleaf pine mast and tick-borne diseases throughout the southeastern U.S. I examined correlative relationships between mast, tick-borne diseases, climate, bird populations, and fire and discussed how a "pine-cone connection" may exist between mast and tick-borne illnesses. Last, chapter five concludes the main findings of this dissertation and provides direction for future research.

CHAPTER II

STAND DYNAMICS INFLUENCE MASTING/RADIAL GROWTH RELATIONSHIPS IN *PINUS PALUSTRIS* MILL.

This chapter was published in *Castanea* Volume. 81, Issue 4 pp. 314–322. The use of "we" and "our" refers to Dr. Paul Knapp and myself who co-authored the manuscript.

2.1 Abstract

Longleaf pine (*Pinus palustris* Mill.) regeneration is dependent on above-average masting (i.e. cone crop) years that occur over 5–7 year cycles. Not understood, however, is how annual cone mast influences radial growth for longleaf pine. Here we collected tree-ring data from one site in South Carolina and two sites in North Carolina to examine: 1) the relationship between longleaf pine mast and radial growth; 2) how timber thinning at one site affected this relationship; and, 3) how previous October–current April PDSI affects mast. We used dendroecological techniques to assemble three radial-growth chronologies and compared annual radial growth to annual mast. We found the strongest negative correlation when mast was lagged one year from radial growth (i.e. mast of year X with radial growth of year X-1), but current-year mast and growth were not significantly correlated. Mast/radial growth relationships were only detectible when radial growth indices < 0.95, suggesting that trees reallocated resources from radial growth to mast production. Thinning improved annual mast yield yet neutralized the negative relationship between mast and radial

growth. Mast correlated with PDSI in the unthinned site but not in the thinned site, suggesting that stand dynamics in the thinned site may have overridden climate / mast relationships. These findings reveal the utility of detecting endogenous factors in radial growth for longleaf pine and the benefits of reducing stand density for improving mast.

2.2 Introduction

Longleaf pine (*Pinus palustris* Mill.) is a long-lived species (> 450 years; Earle 2017) native to the southeastern United States (Frost 2006). Stands of longleaf pine occur primarily on the Coastal Plain and Piedmont physiographic regions, but outlier montane populations occur in the Ridge and Valley region of northern Alabama and Georgia (Peet 2006) and the Uwharrie Mountains of central North Carolina (Patterson and Knapp 2016a). The geographic distribution of longleaf pine has contracted from a pre-European settlement coverage of 37 million ha (Frost 1993) to 1.74 million ha (Oswalt et al. 2012) due to various anthropogenic processes including logging, naval store activities, and fire suppression. Regeneration efforts for longleaf pine are difficult in part due to fire suppression activities that have limited the frequent, low-intensity fires that keep understories open and prevent the establishment of fire-intolerant species (Croker and Boyer 1975). Similarly, reduction in fire frequency has likely altered the germination success associated with episodic masting cycles (Boyer and Peterson 1983) where above-average cone crops occur throughout the species' range every 5–7 years (Wahlenberg 1946), with the largest cone crops (i.e., "bumper years") occurring every 8–10 years (Maki 1952). Spatiotemporal variability in annual longleaf pine mast has been observed throughout the species' range that has been attributed to either

changes in management practices or climatic conditions leading to improved pollination efficiency and cone survival (Croker and Boyer 1975; Boyer 1987, 1997, 1998).

In effort to better understand interannual mast variability, longleaf pine masting data have been collected from eleven permanent sites throughout the southeastern U.S for over 50 years. Mast inventories were initiated by W.D. Boyer during the late 1950s and 1960s and have been recorded by either Boyer or others (Connor *et al.* 2014) through 2016. These data have provided the basis for a better understanding of masting frequency and the geographical consistency of bumper years between inventory sites. Additionally, masting has been shown to correlate significantly with cooler and wetter climatic conditions of the previous autumn–current-year spring (Pederson *et al.* 1999, Guo *et al.* 2016, Leduc *et al.* 2016). Less understood is how changes in site conditions such as timber thinning may influence the interaction between mast and radial growth. Reducing stand density can increase annual mast (Boyer 1979) where open-grown, large-crown trees have the highest cone production (Croker and Boyer 1975; Boyer 1990, Haymes and Fox 2012). To our knowledge, no research investigating tree-ring variability/masting relationships has been examined for longleaf pine. Here we investigate the relationship between variations in longleaf pine mast and annual radial growth pre- and post-timber thinning and compare these results with two control sites that were not thinned. Also, we address the influence previous October–current April Palmer Drought Severity Index (PDSI) has on cone production for the thinned and un-thinned sites. Specifically, we address for longleaf pine: 1) the relationship between annual mast and radial growth; 2) the extent to which a reduction of stand stocking density affects annual mast/radial growth relationships, and 3) the

influence October–April PDSI has on cone production for thinned and un-thinned mast sites. Based on previous mast/radial growth analysis of other species we posit that: 1) negative relationships will exist between longleaf pine mast and annual radial growth and that these relationships are independent of stand density; and, 2) positive correlations between cone crop and October–April PDSI are unaffected by thinning.

2.3 Methods

We collected tree-ring data at two locations in Bladen County, North Carolina and at a third location in Chesterfield County, South Carolina (Figure 2.1). The two North Carolina sites are located at Boyer's collection area in Bladen Lakes State Forest (BLSF; N 34° 44' 15", W 78° 32' 23") and at Jones Lake State Park (JLSP; N 34° 42' 13", W 78° 37' 10"), which is 8.3 km south of BLSF and served as a control. The third site is located at Boyer's collection area in Sandhills State Forest (SHSF; N 34° 32' 43", W 79° 58' 11"), 130 km east of the North Carolina sites and also served as a control. Annual cone mast has been recorded at BLSF for 35 non-consecutive years (1968–74, 1977–79, and 1991–2015), and at SHSF for 46 consecutive years (1969–2015; Brockway 2015). No mast records exist at JLSP. Soil types at the North Carolina sampling sites are classified as "Leon Sand" (Soil Survey Staff 2015), and an examination of 30-year monthly mean temperature and precipitation normals from 4 km X 4 km gridded PRISM data (PRISM Climate Group 2004) revealed climate is nearly identical between sites, differing by an average of 1mm in annual precipitation and 0.1° C in mean annual temperature. Fire regimes have been maintained at the two North Carolina sites on a 2–5 year prescribed-burn interval (Hans Rohr, Pers. Comm. 2015; Figure 2.1C). Therefore, the principal difference between the two North

Carolina locations is that BLSF underwent stand thinning in 1993 where basal area was reduced from 32 m^2/ha to 5.7 m^2/ha (Hans Rohr, pers. comm. 2015). JLSP was chosen as a local control that has not undergone thinning during the study period and matched stocking density to BLSF. Additionally, no thinning during the mast collection period is known to have occurred at the SHSF site, which served as a second control as it has similar climatic (Rhee *et al.* 2008), stand density, and topoedaphic conditions (Soil Survey Staff 2015).

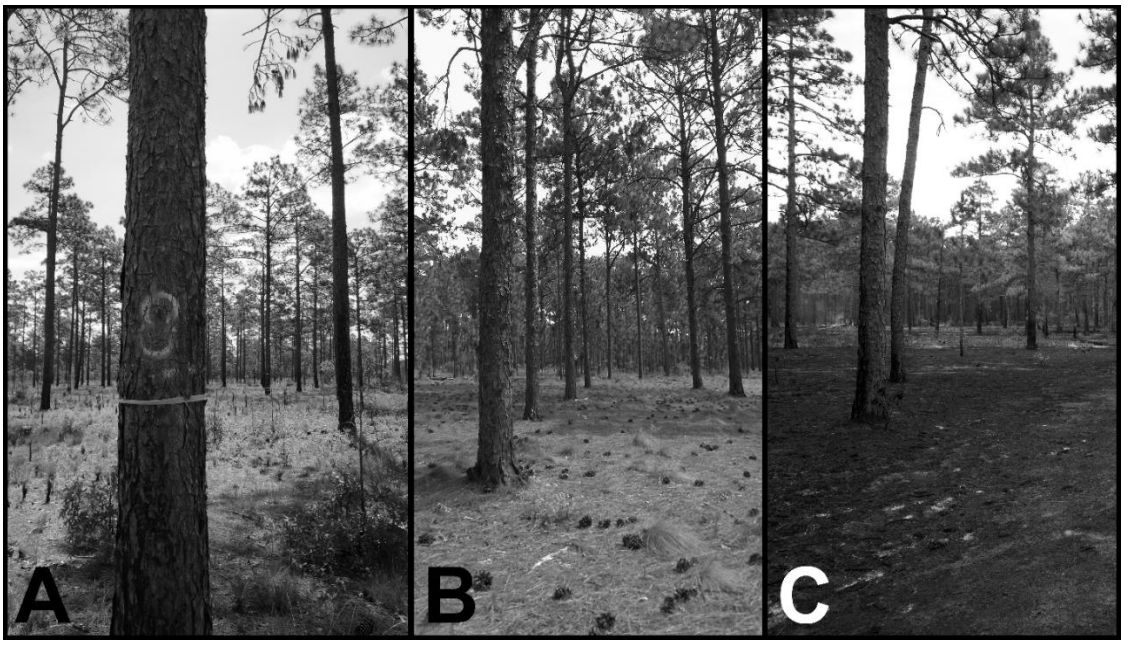

Figure 2.1. A. Cone Collection Site At BLSF Showing Trees Marked For Cone Count In The USFS Study (Not Cored). B. Surface Brown Cones (Indicative Of Prior-Year Mast) At SHSF. C. Recent Prescribed Burn At JLSP.

Using a 5.15 mm diameter increment borer, we obtained two core samples/tree at 1.3 m height from 27 trees at JLSP in September of 2012, 17 trees at BLSF in May of 2015, and 18 trees at SHSF in September 2015. Care was taken to sample evenly throughout each

stand, avoiding trees with box-faced cuts, visible burn scars, or other deformities that may influence radial growth. For all trees, we recorded location, trunk diameter at breast height (dbh), and height. At BLSF and SHSF we were not permitted to sample from the same trees used for the annual mast inventories, but instead selected adjacent trees of similar age/height. Cores were processed following standard laboratory procedures (Stokes and Smiley 1996) for drying, mounting, and sanding each core to reveal ring structure. We used the list method (Yamaguchi 1991) to crossdate each sample. Ring widths from BLSF were manually measured on a Velmex measurement system (Velmex Inc Bloomfield, NY) with Measure J2X software (Voor Tech Consulting Holderness, NH), while JLSP and SHSF ring widths were scanned to 1200 DPI on an Epson scanner and measured using WinDENDRO software (Regents Instruments Québec City, Québec). Crossdating accuracy was validated using COFECHA (Holmes 1983) and we used ARSTAN (Cook and Holmes 1986) to standardize the three chronologies using a negative exponential curve (Cook and Holmes 1986) to produce time-series tree-ring indices with a mean of one. We selected the autocorrelation-free residual chronology from the ARSTAN output as it consistently produced the highest correlations between mast and radial growth and could be used for rank-order analysis between mast and the radial growth indices.

All cone-mast data were log transformed to account for large interannual variability. We used all three residual chronologies to test for statistical relationships between cone mast and radial growth using one-sided Spearman's rank-ordered correlations between mast with both current and previous year's radial growth as longleaf pine cones develop over a 2.5-year process (Brockway *et al.* 2006). Additionally, as Speer (2001) identified, some trees may not

express mast sensitivity, so we individually eliminated tree-ring samples from each chronology that expressed no correlation with mast ($r > -0.2$) to increase mast sensitivity of our chronologies. Data were analyzed over three time periods: full (1968–2014), pre-thinning (1968–1992), and post-thinning (1993–2011) for the BLSF and JLSP sites and for full (1969–2014), pre-thinning (1969–1992) and post-thinning (1993–2014) at the SHSF site. Lastly, we tested for radial-growth/mast detection levels to measure when radial growth is significantly correlated with mast variability. We combined and rank ordered the three residual chronologies from largest to smallest by radial growth with the corresponding mast data. We then repeatedly split the data into two groups using 0.05 radial-growth index reductions (i.e. ≥1.25 vs. <1.25 values; ≥1.20 vs. <1.20 values; etc…) and correlated the two groups with their respective log-transformed mast data.

To test for climate/mast relationships we selected the most persistent climate parameter from Leduc *et al.* (2016) that significantly correlated with mast that happened to be a positive correlation between mast and previous October–current April PDSI. PDSI is a measure of soil-moisture conditions that combines temperature and precipitation where positive values indicate wetter conditions whereas negative values, specifically a PDSI value less than -2, indicates drought. We obtained PDSI data from the National Centers for Environmental Information (NOAA/NCEI 2016) for North Carolina Climate Division 6 (years 1967–2015) for BLSF and JLSP and South Carolina Climate Division 3 (years 1968–2015) for SHSF. One-sided Pearson product moment correlations were used to test the relationship between annual mast and each month of PDSI data.

2.4 Results

The final BLSF chronology consisted of 30 samples, the JLSP chronology had 22 samples, and the SHSF chronology contained 25 samples. Mean (standard error) trunk diameter varied between sites with the smallest mean dbh recorded for BLSF (39.8 (6) cm), followed by SHSF (44.2 (2.5) cm), and JLSP (51.7 (7.1) cm). Mean ages (years (standard error.)) were 76.6 (7.4) for BLSF, 102.5 (39.1) for JLSP, and 93.1 (5.9) for SHSF. A radial-growth surge was detected for the BLSF chronology beginning in 1993—which represented the first thinned year—and persisted for approximately 10 years when growth again approximated that of the nearby JLSP chronology (Figure 2.2, dotted line). During the decadal growth surge, four of the five largest masting years occurred. No growth surges existed for either the JLSP or SHSF chronologies during the same period. Mast at SHSF correlated with prior-year October and January–March PDSI, yet BLSF had no significant correlations with PDSI data for the same months (Table 2.1).

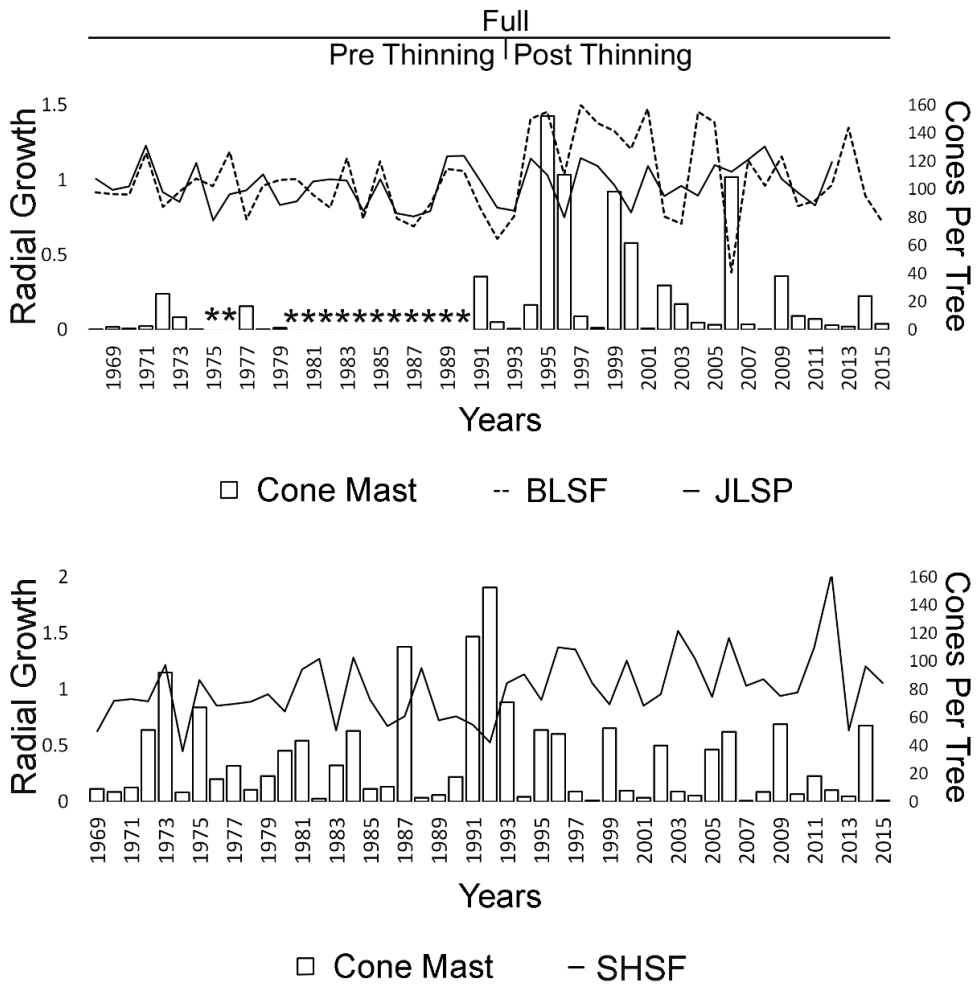

Figure 2.2. (Top) Time Series Of Lagged, Standardized Tree-Ring Growth At BLSF (Dashed Line) And JLSP (Solid Line) With Annual Cone Masting Data (Columns) From BLSF During 1968–2015. Asterisks Indicate Missing Mast Years For BLSF (1975–1976, 1980–1990). (Bottom) Time Series Of Lagged, Standardized Tree-Ring Growth At SHSF (Solid Line) With Annual Cone Masting Data (Columns) During 1969–2015.

Table 2.1. One-Sided Pearson Correlation R Values Between Mast At BLSF (1968–74, 1977–79, And 1991–2015, N = 35) And SHSF (1969–2015, N = 46) And Previous October To Current April PDSI. * = $P < 0.05$, ** = $P < 0.01$

	Oct	Nov	Dec	Jan	Feb	Mar	Apr
BLSF	0.169	0.069	0.030	0.063	0.007	-0.112	-0.127
SHSF	0.239	0.248*	0.240	0.279*	0.325*	0.341**	0.225

Mast from BLSF was correlated with both the BLSF and JLSP chronologies whereas mast from the SHSF was correlated only with the SHSF chronology. Correlations between annual mast and each residual chronology for the three periods (Table 2.2) were strongest when growth was lagged one year (i.e. radial growth of year X-1 was correlated with mast of year X). For the full period (i.e., 1968–2014) radial growth at the JLSP (r = -.29) and SHSF (r = -.56) were negatively correlated ($p < 0.05$) with annual mast, but the BLSF chronology was not ($p > 0.05$). During the pre-thinning period (1968–1992) the BLSF expressed a significant, negative relationship that became non-significant post-1992 after thinning occurred (Table 2.1). The JLSP control site had negative correlations between mast and the residual chronology for the pre-and post-thinning periods, but the pre-thinning negative correlation was non-significant. Finally, the radial-growth threshold test revealed no significant relationship ($p > 0.05$, n = 97) with mast when radial growth index values were ≥ 0.95. Conversely, when radial-growth index values were < 0.95, correlations with log-transformed mast were significant (r = -0.30, p = 0.02, n = 64). Similarly, when radial-growth index values were ≥ 0.95 there was a 29% occurrence of an above-average mast year, yet when radial-growth index values were < 0.95 the occurrence (57%) of an above-average mast year doubled.

Table 2.2. Spearman Rank-Order Correlations Between The Residual Chronologies Lagged 1 Yr (Left) And Current Year (Right) With Annual Cone Mast For The Three Periods Full (1968–2014), Pre-Thinning (1968–1992), And Post-Thinning (1993–2014). Mast Data From BLSF (1968–74, 1977–79, And 1991–2015, N ¼ 35) Were Correlated With The Radial Growth Chronologies For Both BLSF And JLSP, And Mast Data From The SHSF (1969–2015, N ¼ 46) Were Correlated With Radial Growth From SHSF

	One-Year Lag			**Current**		
Site	Full	Pre-thinning	post-thinning	Full	Pre-thinning	Post-thinning
BLSF	-0.081	-0.552*	-0.187	0.095	-0.329	0.123
JLSP	-0.293*	-0.291	-0.585**	-0.048	-0.007	-0.232
SHSF	-0.555**	-0.418*	-0.54**	-0.101	-0.054	0.058

2.5 Discussion and Conclusion

The largest masting years coincided with the post-thinning growth surge at BLSF (not observed at JLSP or SHSF) suggesting that the stand-density reduction created conditions favorable for larger annual cone crops. These results are consistent with the findings of Croker (1973) who found reduced stocking density improved annual longleaf pine mast and that less-dense stands tend to produce more longleaf pine cones per hectare (Croker 1973). Similarly, thinned red oak (*Quercus rubra*) stands in New England also have shown increased mast post-thinning (Healy 1997, Healy *et al.* 1999).

Our results do not indicate that negative relationships between longleaf pine mast and radial growth remain constant with stand density changes. The only significant relationships between mast and radial growth existed when prior-year radial growth was

correlated with current-year annual mast. Additionally, radial growth/masting relationships changed from significantly negative to non-significant following thinning, suggesting a threshold where resources are sufficiently abundant for increased mast without reduced radial growth. Resource-tracking theory (Kelly 1994), which explains how variations in annual mast are directly attributable to resources available to trees (i.e. favorable climate), may account for the observed increase in mast from thinning. This theory, however, does not explain how the amount of additional resources available outweighed the taxing effect that the large mast produced. Overall, when prior-year radial growth index values remained ≥ 0.95 no radial growth index/mast crop relationship existed. Conversely, prior-year radial-growth index values of < 0.95 were negatively correlated to current-year mast, and current-year mast crops were twice as likely to be above average compared to years with values ≥ 0.95. These results suggest that a mast/radial growth influence is more likely to be detected during years when radial growth is below average and limited by other factors controlling growth such as climate. This relationship also may explain why the control chronologies (i.e., SHSF and JLSP) maintained a negative relationship with mast during the pre- and post-thinning periods, but the BLSF chronology did not despite the great environmental similarities among sites.

Positive correlations between cone crop and October–April PDSI were inconsistent between mast sites. We found this relationship at SHSF, but not at BLSF, possibly due to stand conditions overriding the influencing of PDSI. Similar to previous climate/mast studies for longleaf pine, our results at SHSF confirm those of Pederson *et al.* (1999) and Leduc *et al.* (2016) that moisture conditions the previous October–current April positively

influence mast. Our results are also supported by Guo *et al.* (2016) who found warmer July–August temperature and wetter October–November are associated with improved cone production. These results suggest the influence of thinning improves mast beyond the influence of favorable climatic conditions.

These masting/radial-growth results for longleaf pine are consistent with what has been identified between tree-ring growth and mast for a number of dendromastecology studies (e.g., Speer 2001, Drobyshev *et al.* 2010, 2014). Negative associations between mast and growth have been identified for several oaks (*Quercus*) (Speer 2001), beech (*Fagus sylvatica* L.; Holmsgaard 1958, Drobyshev *et al.* 2010, 2014), Douglas fir (*Pseudotsuga menziesii* Mirb.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), and western white pine (*Pinus monticola* Dougl.; Eis *et al.* 1965), as well as a suite of other species(Koenig and Knops 1998). These studies suggest that trees allocate resources (i.e. carbon) from radial growth to increase mast. One-year lagged mast/growth relationships exist for beech (Drobyshev *et al.* 2014; Hacket-Pain *et al.* 2015) when radial growth was examined the year following mast. As longleaf pine cones require 2+ years of development (Brockway *et al.* 2006) we posit the greatest strain on radial growth occurs the year prior to mast.

Our results may be useful for understanding the influence endogenous factors have on longleaf pine radial growth and have applications for land managers seeking to improve longleaf pine mast. One caveat with interpreting our results into management is that due to the lack of replication of sampled sites our results might not be widely generalizable. Boyer (1990) suggests trees in the 38–48 cm dbh size class produce on average 65 cones/year. Trees in a smaller size class (25–33 cm dbh) produce 15 cones/year, suggesting a benefit of

managing a stand for larger-diameter longleaf pine to optimize cone production. Similarly, Haymes and Fox (2012) found that open-grown, larger-diameter trees tend to produce the greatest number of cones per year. The three stands sampled in this study all are within the optimal dbh size-class range and in theory should be at prime cone production. Additionally, the best seed production occurs in stands that range in density of 6.9–9.2 m^2/ha (Boyer 1979), a finding that might have influenced the thinning of BLSF from an overstocked 32 m^2/ha to 5.7 m^2/ha. The decade following thinning at BLSF witnessed four of the top five largest seed crops further confirms the benefit of reducing stand density.

The greatest longleaf pine cone production occurs at sites with trees > 30 years old that have well-formed crowns and at least 25cm dbh boles (Croker and Boyer 1975) and these conditions are exceeded at BLSF and SHSF. While cones develop over a three-year process, identifying wetter autumn–spring conditions may indicate larger cone crops, yet other temperature and precipitation variables are also known influence mast (Leduc *et al.* 2016). Thus, our results are consistent with others (Croker and Boyer 1975, Boyer 1979, 1990, Haymes and Fox 2012) and suggest land managers may improve cone crop from stands thinned to optimal stocking density within the appropriate trunk diameter size class. Lastly, these results may be useful in recognizing the potential modifying effects of annual mast to climate/growth relationships of longleaf pine, particularly how drought and mast events may elicit similar growth responses.

CHAPTER III

LONGLEAF PINE CONE/RADIAL GROWTH RELATIONSHIPS FROM INDIVIDUAL TREES AT SIX LOCATIONS IN THE SOUTHEASTERN U.S.

This chapter is a manuscript that will be submitted to *Dendrochronologia*

3.1 Abstract

Longleaf pine (*Pinus palustris* Mill) cone production is counted annually at eleven locations throughout the species' range beginning in 1958. These data have been useful for understanding spatiotemporal patterns in cone production that are used in natural regeneration efforts. Variations in annual mast are known to affect growth rings in numerous tree species, and not well understood is how this relationship operates for longleaf pine. This research examines the relationship between longleaf pine cone data and tree-rings from an individual-tree perspective. We examined tree-ring data from the actual trees used in the multidecadal cone study and were granted proprietary cone data from each individual tree at six sites in four locations. We used these data in regression models to examine whether the inclusion of mast data improved explainable variance in climate data. We found that longleaf pine cones were correlated with radial growth over its 2+ year development cycle. The narrowest radial growth rings were more associated with above average mast, and radial growing during years that coincided with the largest cone-crop class (bumper, > 100

cones per tree) were statistically narrower than any other cone class. The inclusion of mast data did not improve R^2 values in regression analyses. Due to the variability of mast between trees in each stand, and with bumper years occurring infrequently, radial growth chronologies assembled from longleaf pine for dendroclimatic purposes are not likely to be influenced by reproductive strain.

3.2 Introduction

Longleaf pine forests once spanned an estimated 37 million hectares (Frost 1993) of the coastal plain and piedmont physiographic regions of the American Southeast. A fraction of this forested landscape remains today (1.74 million hectares, Oswalt *et al.* 2012) as various anthropogenic processes including fire suppression, deforestation without replanting, animal grazing, and other land-use changes (Frost 2006) were widespread. Currently, a reversal in longleaf forest decline is underway largely due to replanting. Roughly one-fourth of all longleaf in existence today is planted and 84% of it less than 20-years old (Gouldin *et al.* 2017). Reforestation strategies for longleaf pine include planting containerized seedlings on clear-cut tracts or thinning techniques that remove unwanted vegetation and leave behind a number of sexually-mature trees capable of producing their own seed source (Brockway, Outcalt and Boyer 2006). Due to the infrequent nature of adequate longleaf pine cone crops (i.e. mast), once every five-to-seven years (Wahlenberg 1946), cost-effective reforestation techniques that utilize local seed trees need be timed to coincide with large cone crops (i.e. masting events).

In an effort to better understand the frequency of longleaf pine mast, cone production has been monitored throughout the longleaf pine range at a number of locations

as part of a long-term regeneration study called the "Longleaf Regeneration Trials" Connor *et al.* 2014). Beginning with annual cone counts in the Escambia Experimental Forest in Southern Alabama in 1958, annual cone counts have expanded to includes 11 sites that range from North Carolina to Louisiana as of 2016 (Brockway 2016). At each stand the number of green cones and conelets, indicative of next year's cone crop, are counted for ≥ 10 trees and averaged to produce a stand average cone crop. These results are published each spring and disseminated to foresters to help guide management techniques (e.g. natural regeneration) dependent on expected seed release from the cones during autumn. Results from this research have shown that longleaf pine cone crops vary year-to-year but also spatially between sites (Boyer 1987). The 51-year regional average cone production is 28 cones per tree (Brockway 2016). Half of all years since 1966 have produced > 25 cones per tree, and > 50 cones per tree for roughly one tenth of all years (Brockway 2016). These values are important due to the number of cones needed for successful regeneration: 750–1000 cones per acre depending on stocking density (40–75 cones per tree (Boyer 1997, Boyer 1993)). Genetics influence the number of cones produced for individual trees, yet size, crown class, stand density and site quality are all important (Brockway *et al.* 2006). Some variation in annual cone crop is believed to be influenced by weather; however, cones develop over two years and showing linkages between weather variables and cone production is difficult. Pederson (1999) examined monthly weather variables as they pertain to cone crop at the Escambia Experimental Forest, and more recently this research has expanded to all sites (Leduc *et al.* 2015, Chen *et al.* 2016b, Guo *et al.* 2016). While longleaf cone production is complex, warmer and wetter conditions during the two years of cone development have a

positive influence on cone crop (Shoulders 1967, Pederson *et al.* 1999, Leduc *et al.* 2015). While a general understanding exists regarding the frequency of masting years and the variables that influence longleaf pine cone crops, less understood is how variations in annual cone crop influence internal growth dynamics such as radial growth rings and the extent of spatial variability in mast crop.

A number of studies have examined the influence annual mast has on annual, radial growth rings of trees. As trees trade-off resources (i.e. carbon) from radial growth in the trunk to reproduction in the canopy, linkages have been made that show negative relationships between annual mast crop and annual radial growth (Holmsgaard 1958, Eis *et al.* 1965, Woodward *et al.* 1994, Koenig and Knops 1998, Hacket-Pain *et al.* 2015). Speer (2001) and Drobyshev *et al.* (2014) have explored these relationships and used Oak and Beech tree-ring data to produce multi-century reconstructions of annual mast. Hacket-Pain *et al.* (2015) combined mast with climate data to better explain variance in beech growth rings. These studies provide the most recent evidence for the feasibility of time series analysis of mast on tree rings yet are limited to hardwood species. Woodward *et al.* (1994) examined relationships between mast, climate, and radial growth of subalpine fir and mountain hemlock and found larger and average mast crops had a larger reduction in radial growth than below average crops for these conifer species. In a synthesis on masting and tree rings, Hacket-Pain *et al.* (2016) underscore the importance for understanding how trees allocate resources to reproduction, and in particular how mast imprints growth rings in ways similar to climate extremes (i.e. drought). At present, research that incorporates mast into climate reconstructions is limited in part due to the paucity of multidecadal mast datasets. However,

if available, these data can be useful to interpret variations in radial growth not attributable to annual climate and in turn may improve the accuracy of a tree-ring based climate reconstruction.

Previously, I explored mast/tree-ring relationships of longleaf pine using USFS mast counts and tree-ring data collected from two masting sites in North and South Carolina. I uncovered a negative relationship between log-transformed longleaf pine mast and residual radial growth of the previous year. The North Carolina masting site was thinned to a lower stocking density and I showed how the reduction of stand density temporarily ameliorated mast/radial growth relationships. While limited in scope, my previous research showed a relationship exists between longleaf pine mast and radial growth that is sensitive to changes in stand density.

Annual growth rings of longleaf pine are principally influenced by temperature and precipitation from mid to late growing season with much of the variability present in latewood growth (Devall, Grender and Koretz 1991, Foster and Brooks 2001, Henderson and Grissino-Mayer 2009 Patterson *et al.* 2016). The fidelity between longleaf pine growth rings and climate has been useful for developing tree-ring based reconstructions of tropical cyclone precipitation (Knapp *et al.* 2016), drought (Ortegren 2008), and streamflow (Harley *et al.* 2017). Not evaluated in these studies are how variations in annual mast may influence climate-growth relationships or tree-ring based climate reconstructions. To this end, this research examines longleaf pine mast/radial growth relationships at six sites in four locations in order to determine: 1) how annual mast influences radial growth at masting sites in Alabama, Florida, and Georgia; and 2) if linear regression models that pair mast and ring

growth data are useful in explaining variance in climate data. Herein, I present six newly developed chronologies from the exact trees whose cones are counted annually, and I paired these data with proprietary cone data from each individual tree. I explore how annual cone production influences radial growth, and develop linear models to explain variance in Palmer Drought Severity Index (PDSI, Palmer 1965). If the inclusion of mast data with tree ring data is influential in explaining variations in PDSI, future use of these data may help the predictive power of multi-century climate reconstructions using longleaf pine.

3.3 Methods

3.3.1 Cone Count Sites

As of 2016, the USFS counts annual cone production at 11 sites in the longleaf pine range. I selected four sites for this study based on data completeness and recommendations by Dr. Dale Brockway that included: The Escambia Experimental Forest in Escambia County, Alabama; Blackwater River State Forest in Santa Rosa County, Florida; Eglin Air Force Base (AFB) in Okaloosa County, Florida; and the Joseph W. Jones Ecological Research Center in Baker County, Georgia (Figure 3.1). The Escambia Experimental Forest, located in southern Alabama, is managed by the USFS through a 99-year lease with the T.R. Miller Mill Company. The 1214-acre forest was established in 1947 to study various longleaf regeneration and management methods (Connor *et al.* 2014). Cone-production inventories were initiated here in 1958 and later expanded to 10 similar shelterwood stands throughout the longleaf pine range beginning in 1966 (Connor *et al.* 2014). At Escambia, two cone-count sites were sampled: the "Farm Forty" stand and the "Croker Pond" Stand approximately 2-km distance from one another. Similar to Escambia, I sampled from two stands at Eglin

AFB that were known as the "Rattlesnake" stand and the "Boondocks" stand that were roughly 20-km distance from one another. Both The Blackwater River State Forest stand and the Jones Center stand contained one cone-count site. Therefore, I am treating each stand as a separate site for a total of six sites.

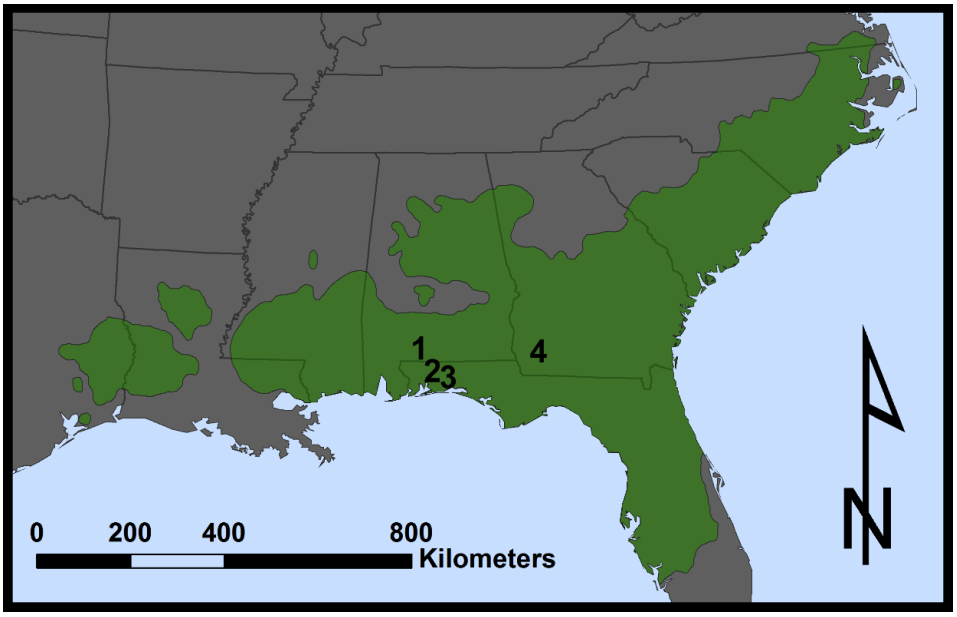

Figure 3.1. Map of The Four Cone Count Locations Within The Longleaf Pine Range (Green Polygon): 1) The Escambia Experimental Forest (Containing The Croker Pond And Farm Forty Stands), 2) Blackwater River State Forest, 3) Eglin AFB (Containing Rattlesnake And Boondocks Stands), And 4) The Joseph W. Jones Ecological Research Center

3.3.2 Sampling Procedures

All fieldwork was undertaken during December of 2015. I was accompanied by Dr. Dale Brockway in the field to identify marked trees in the cone-count study. Rather than randomly sampling trees in each stand, as was the procedure in my previous research (Chapter 2, Patterson and Knapp 2016b) I was permitted to sample from the exact trees that

are counted annually (e.g. Figure 3.2). Four of the stands contained ten trees, whereas there were 11 trees at Jones and 12 trees at Farm Forty. At time of sampling tree nine at the Rattlesnake stand was dead, however Dale Brockway confirmed the tree was living at time of cone count (April) in 2015. Similarly, tree ten at the Boondocks stand was dead at time of cone count in April 2016, yet was living at time of sampling in December 2015. Therefore, in total I sampled from a total of 63 trees for this study. Two core samples were obtained from opposing sides of each tree using 5.15mm increment borers. When a core sample was damaged on extraction a third was extracted. Each tree was georeferenced and trunk diameter at breast height (cm) and crown height (m) were obtained using diameter tape and a digital laser rangefinder respectively.

Figure 3.2. Tree Number Eight At Blackwater River State Forest. Trees At Each Site Had Painted Numbers And Were Sometimes Flagged (See Above) With The Exception Of The Jones Center That Used Metal Tags For Preserving The Aesthetics Of A Natural Forest (Steve Jack, Jones Center, Pers. Comm.).

3.3.3 Laboratory Procedures

Samples were processed in the Carolina Tree-ring Science Laboratory using standard dendrochronological techniques (Stokes and Smiley 1996). Following processing, all samples were visually crossdated using the list method (Yamaguchi 1991) and scanned to 1,200 dpi using an Epson scanner and measured with WinDENDRO software (Instruments 2012). WinDENDRO provided three ring-width measurements that included total ring width

(hereafter totalwood), earlywood, and latewood. Totalwood ring width comprises both early and latewood measurements, the latter two indicative of cellular growth taking place earlier and later in the growing season. Ring-width measurements were compiled into site chronologies and crossdating accuracy was evaluated using the program COFECHA (Holmes 1983).

3.3.4 Cone Data

The official, annual USFS cone report provides the average number of cones produced for 11 locations in the longleaf pine range based on averages obtained from the 10–12 trees per study site (combining multiple sites for Escambia and Eglin AFB). The number of green cones and conelets (indicative of the following year's cone crop) are visually counted with binoculars each February–April (see Brockway 2016 for details on cone-count protocol). These data are publically available and were previously used in Patterson and Knapp (2016b) to establish the relationship between longleaf pine mast and radial growth. At that time, I was not permitted to remove core samples from the individual trees used in the cone-count survey for the cone-count stands in North and South Carolina. For the current project, I was permitted to sample from the actual trees used in the multidecadal study, and Dr. Brockway graciously provided the accompanying individual cone data for all 63 trees. These raw data existed from 2007–2016 for all sites, however 2008 was missing from four sites, and the Jones site had complete data for 2003, 2005–2016 (Table 3.1). Digital records of individual cone data did not exist prior to 2003, and paper files could not be found at the time of this study (Dr. Dale Brockway, pers. comm.).

Table 3.1. Number Of Trees Sampled And Individual-Tree Cone-Data Availability For Each Site.

Site Name	No. trees	Data availability
Croker Pond	12	2009-2016
Farm Forty	10	2007, 2009-2016
Blackwater	10	2007, 2009-2016
Rattlesnake	10	2007, 2009-2016
Boondocks	10	2007, 2009-2016
Jones Center	11	2003, 2005-2016

3.3.5 Analyses

I began testing for relationships between longleaf pine ring widths and annual cone production for each tree using raw ring widths. For each tree, I averaged raw ring widths from the two core samples to create one measurement series per tree. I followed this procedure for all the three measurements: totalwood, earlywood, and latewood. Longleaf pine cones develop over a two-year process (Brockway *et al.* 2006) therefore I tested how growth of a particular year was influenced by cone production the same year, but also how growth of a particular year related to cone production 1–2 years into the future. I was also interested in a "hangover" effect to see if a large cone crop influenced ring growth the year following. To test for these relationships, cone data for each tree were aligned with their accompanying ring-width measurements in the following sequence of pairings: same year (e. g. Cones of 2015 with ring width of 2015), one and two-year lag (e.g. Cones of 2015 with ring width of 2014, 2013), and one-year post (e.g. Cones of 2016 with ring widths from 2015). Next, I combined these pairings into columns that contained all cone year/ring-width combinations for all trees in each site. This process was repeated at each site for the three ring-width measurements and for all four time comparisons. For each site I had four

totalwood, latewood, and earlywood relationships to be examined. I explored the relationship between the number of cones produced and raw ring widths using two-sided Pearson's product-moment correlations for all sites and time comparisons.

After site-based analysis I examined how cone crops of varying sizes influence mean ring width. One method I used to explore this relationship was to first combine all cone/ring-width pairs from the six sites into one super group each for totalwood, latewood, earlywood. I only examined this relationship for the same-year pairing described above. I then computed z-scores for raw ring width and number of cones produced. Next, I ranked radial growth by z-score and examined the frequency for above or below-average cone crop z-score as it related to radial growth. The other method I used involved using the official USFS cone reports to classify cone crops into five categories based on average cones produced per tree that included: failed (0–9), poor (10–24), fair (25–49), good (50–99), and bumper (100+). All crop–ring width pairs were assigned a categorical group number (1–5) based on failed–bumper crop categories. I explored differences in mean ring width between USFS derived cone-crop groups using one-way analysis of variance (ANOVA) tests. ANOVA tests are omnibus, providing an F-test statistic that describes whether there is a statistical difference in means and variance of more than two groups (cone classes). In order to determine which groups were statistically different from one another I applied Tukey's honest significance difference (HSD) post-hoc tests with all ANOVA tests.

I tested whether mean sensitivity of individual trees was related to cone production. Mean sensitivity is a measure of year-to-year variability in ring growth where higher values indicate a greater potential for relationships to climate or annual mast. These values are

produced from the COFECHA output and are available for each tree in the dataset. As cone production varies considerably by site and year, I needed to standardize each tree's contribution to the overall site production of cones to balance high and low producing sites for combined analysis. To do this I summed the total number of cones produced by each tree for all available years, then divided each tree's total from the site total (total of totals). As a result, I developed a percentage of each tree's contribution to the total mast of each site during the observed study years. Next, I averaged mean sensitivity between the 2–3 individual cores of the same tree to produce one mean sensitivity value for each tree. I correlated mean sensitivity values with each tree's cone contribution for all 63 trees using Pearson's one-sided correlations. I repeated these analyses for the three ring measurements.

My last exploration of mast–ring-width relationships tested whether the inclusion of mast data improves explainable variance when examining the relationship between radial growth and climate. I examined this relationship for all six sites and for all three growth measurements. Each chronology was standardized using the program ARSTAN (Cook and Holmes 1986). I standardized each chronology using a cubic smoothing spline with a frequency response of 50% at two thirds (67%) the length of each sample in the chronology. This standardization removes age-related growth trends, yet is flexible to also remove variance related to forest disturbances such as suppression and release events not attributed to annual climate and masting. The program ARSTAN produces indexed growth chronologies with a mean of one. I selected the ARSTAN chronology, which has had all autocorrelation removed from each individual sample, then modeled and reintroduced at the stand level (Speer 2010) for all analysis. Next, I downloaded Palmer Drought Severity Index

(PDSI; Palmer 1965) data for all months from 1895–2015 for Florida climate division one, Alabama climate division seven and Georgia climate division seven. I examined the strength of Pearson's correlation coefficients between the ARSTAN chronologies for totalwood, latewood, and earlywood samples from the six and monthly PDSI in for the climate division of residence. The months of July–September (March–May) consistently produced the strongest correlation coefficients ($r > 0.4$) for total and latewood (earlywood), therefore I averaged these months and used average PDSI exclusively. I then acquired the published masting data from the USFS (Brockway 2016) for average annual mast produced by site. I used simple linear regression models to explore the amount of variance that can be explained in averaged July–September PDSI, as indicated by R^2 values, using the ARSTAN chronologies and the inclusion or omission of annual averaged mast data as predictors. Therefore each regression model uses the ARSTAN chronology or the ARSTAN chronology and Cones as predictors for the response average PDSI:

e.g.: Average PDSI = Latewood or Average PDSI = Latewood + Cones

Finally, I examined whether individual trees that significantly correlated with climate were correlated with overall cone production. I explored this relationship by correlating the *r* values of individual samples that produced significant correlations with averaged PDSI with total individual cone production for all years of available cone data using Pearson's product moment correlations.

3.4 Results

The number of cones produced varied considerably among trees and between sites. While I did not test the variability in the number cones produced between trees within each site, there are individuals that are larger contributors relative to some trees that consistently produce small cone crops (Figure 3). The right-skewed distribution of each tree's total cone contribution indicates that three individual trees, one at Jones, Boondocks, and Blackwater River, contribute greater than 40% of the total volume of cones produced for their respective site. This finding suggests that cone production by individual trees is not equitable, and that some individuals within each stand have a disproportionately larger contribution relative to others. Similarly, Figure 3.3 shows the number of cones produced for all trees and years in my dataset (n = 521). There were 186 cases where zero cones were produced, and 306 cases of a failed crop (0–9 cones produced). There were three extreme years where 542, 700, and 854 cones were produced by a particular tree in a stand.

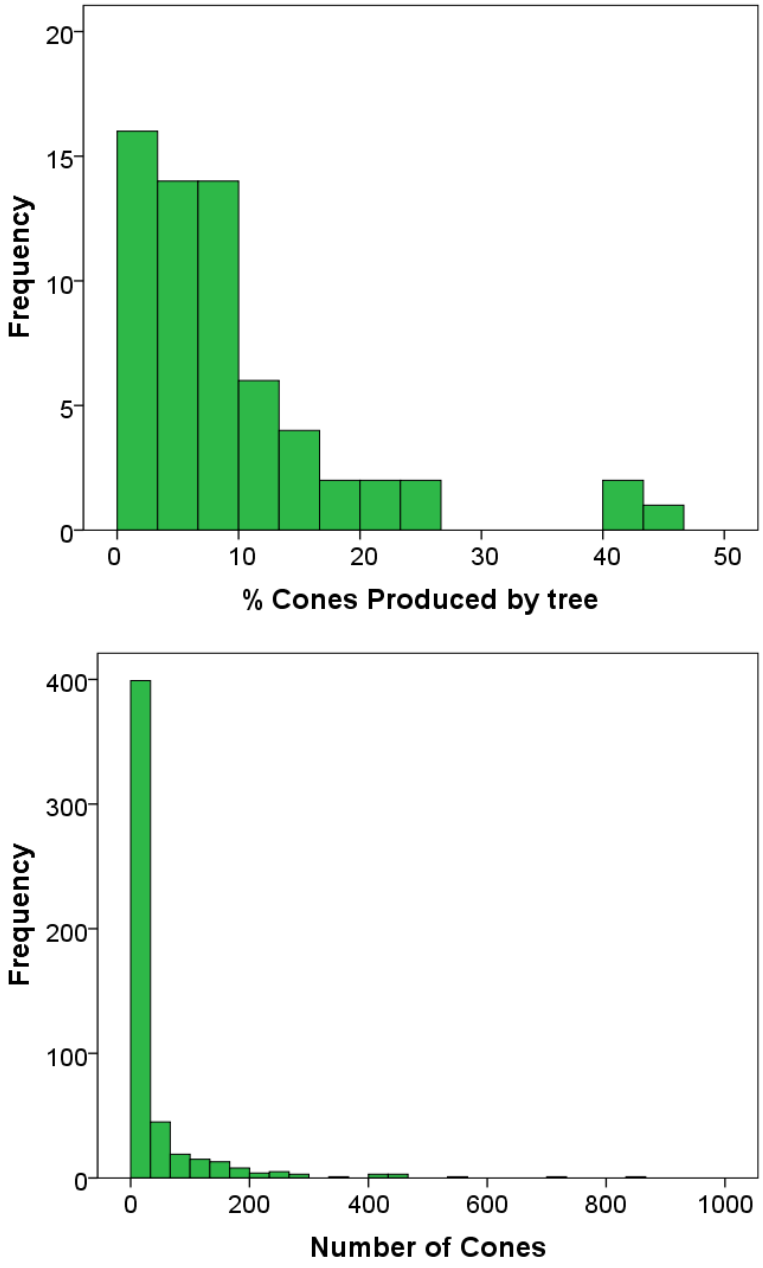

Figure 3.3. Top: Frequency Distribution Of The Percent Cone Contribution For Each Tree (N=63). Bottom: Number Of Cones Produced For A Particular Tree On A Given Year For All Trees And Years In My Dataset (N = 521).

A total of 63 trees were sampled in this study from six sites. Table 3.2 provides chronology statistics for each site based on the results from the program COFECHA. Mean age for all chronologies were < 100 years at date of sampling (2015) indicating these stands are all second growth. The oldest trees of all 63 in the study dated to 1872 at curvature. Interseries correlation values, a measure of the common-signal strength of a chronology, were highest for totalwood at all sites except the jones center where interseries correlation values for latewood were slightly higher. These values were evenly split between sites for earlywood and latewood with three sites expressing stronger values for earlywood over latewood. Mean sensitivity values, a measure of year-to-year variability between growth rings, were strongest for latewood at all sites, and similar to interseries correlation were split 3-3 between totalwood and earlywood chronologies for the next strongest.

Table 3.2. Summary Statistics From COFECHA For The Six Sites. IC= Interseries Correlation And MS = Mean Sensitivity. Age = Average Age. TW = Totalwood, LW = Latewood, EW = Earlywood

		TW		EW		LW	
	Age	IC	MS	IC	MS	IC	MS
Farm Forty	89.9	0.523	0.296	0.468	0.307	0.447	0.439
Croker Pond	78.5	0.588	0.302	0.514	0.32	0.582	0.455
Blackwater	69.8	0.689	0.298	0.623	0.323	0.576	0.439
Boondocks	80.3	0.606	0.316	0.468	0.314	0.603	0.472
Rattlesnake	98.8	0.65	0.338	0.598	0.335	0.59	0.496
Jones Center	91.4	0.56	0.396	0.473	0.395	0.567	0.572

Site-based correlations between raw ring width and number of cones produced varied between sites, years, and ring-width measurements (Table 3.3). The sites where these correlations were strongest included the two Escambia sites (Farm Forty and Croker Pond)

and Blackwater River. The two Eglin AFB sites (Boondocks and Rattlesnake) had the fewest significant correlations, the Boondocks producing no significant correlations. Differences also existed in the analysis of the years when growth and cones are correlated. Longleaf pine cones develop over a two-year process, and there is a strong positive correlation between raw ring width and cones when lagged two years. Few significant correlations existed when cones were lagged one year; however cones and growth of the same year were negatively correlated with directionally consistent results that were not always significant. Two sites, Rattlesnake and Blackwater River expressed significant correlations between ring widths and cones of the previous year yet the direction of these relationships were opposite and likely spurious. Last, the three growth measurements expressed differences in their correlation strength with cones. At Jones and Croker Pond, latewood widths produced the strongest correlations with cones of the same year and when lagged two years. At Farm forty and Blackwater River, earlywood widths were the strongest when correlated with cones lagged two years. Ring width correlations with cones of the previous year were strongest in earlywood, yet were only present at Farm Forty.

Table 3.3. Pearson's Product Moment Correlations Between The Raw Ring Widths And Cones By Site For The Three Growth Measurements. Statistically Significant Results Are Bolded And Are Flagged (P < 0.05 = *, P < 0.01**). Minus 2 Indicates Growth Of Two-Years Prior Correlated With Cones Of Current Year. Minus One Indicates Growth Of Prior Year Correlated With Cones Of Current Year. Plus 1 Indicates Growth Of Future Year Correlated With Cones Of Current Year. TW = Totalwood, LW = Latewood, EW = Earlywood

			EW	
	Minus 2	Minus 1	Same	Plus 1
Jones	0.142	-0.042	-0.108	-0.170
Croker	**0.393****	0.101	-0.214	-0.211
Farm Forty	**0.308****	**0.227***	0.119	0.029
Boondocks	-0.120	-0.138	-0.087	-0.046
Rattlesnake	-0.047	-0.013	-0.116	**-0.334****
Blackwater	**0.269***	0.027	-0.040	**0.251***
			LW	
Jones	**0.244****	0.100	**-0.173***	0.079
Croker	**0.593****	0.115	**-0.307****	-0.145
Farm Forty	**0.262***	0.193	-0.081	0.053
Boondocks	0.068	-0.006	-0.107	-0.021
Rattlesnake	0.084	-0.077	-0.205	-0.196
Blackwater	0.196	-0.049	-0.154	0.205
			TW	
Jones	**0.208***	0.032	-0.149	0.032
Croker	**0.533****	0.115	**-0.281***	-0.185
Farm Forty	**0.308****	**0.224***	0.018	0.044
Boondocks	-0.004	-0.076	-0.113	-0.038
Rattlesnake	0.030	-0.047	-0.172	**-0.294***
Blackwater	**0.238***	-0.015	-0.106	**0.249***

When I combined all raw ring-width/cone-crop pairs I found that more above average cone years (mean = 37 cones per tree) were associated with narrower growth rings (negative z-scores) than wider growth rings (Table 3.4). The narrowest growth rings (≤ -1 SD) were twice as likely to be associated with an above average cone years as the widest growth rings (≥ 1 SD) for totalwood and latewood.

Table 3.4. Percentages Where Radial Growth Z-Scores Were Associated With Above Average (Mean 37) Cone Years. SD = Standard Deviation. TW = Totalwood, LW = Latewood, EW = Earlywood

TW				
≤ -1 SD	-1 SD – -0.5 SD	-0.5 SD –.5 SD	0.5 SD – 1 SD	≥ 1 SD
28.1	26.1	22.7	18.9	13.3
EW				
25.7	21.6	24.1	19.6	18.2
LW				
27.8	29.3	20.2	22.7	10

When ring width/cone pairs were grouped by their accompanying cone class (failed–bumper) significant pairwise differences existed between ring widths for the three ring-width measurements (Table 3.5, Figure 3.4). More pairwise differences existed for totalwood than the other two growth measurements, and the majority these differences existed in the two-year lag relationship. The most common pairwise differences were between the smallest cone crop class (Fail, 0–9 cones per tree) and the largest (Bumper, ≥ 100 cones per tree); however, the direction of this difference depended on the relationship (e.g. same vs. two-year lag). Figure 3.4 helps illustrate these mean ring widths graphically and displays the differences in

mean largest cone crop classes. Interestingly, variation in mean ring width seems to increase from the smallest class sizes to the largest, with differences in mean ring with for bumper years being the largest.

Table 3.5. Significant ($P < 0.05$) Tukey's Pairwise Comparisons Between Cone Crop Class. Cone Crop Classes Are Defined By The USFS As Follows Failed (0–9), Poor (10–24), Fair (25–49), Good (50–99), And Bumper (≥ 100).

	Minus 2	Minus 1	same	Plus 1
EW	Failed–Fair Failed–Bumper Poor–Bumper Good–Bumper			Failed–Fair
LW	Failed–Bumper Poor–Bumper Good–Bumper		Failed–Bumper Poor-Bumper	Failed–Fair
TW	Failed–Poor Failed–Bumper Poor–Bumper Good–Bumper		Failed–Bumper Poor–Bumper	Failed–Fair Fair–Bumper

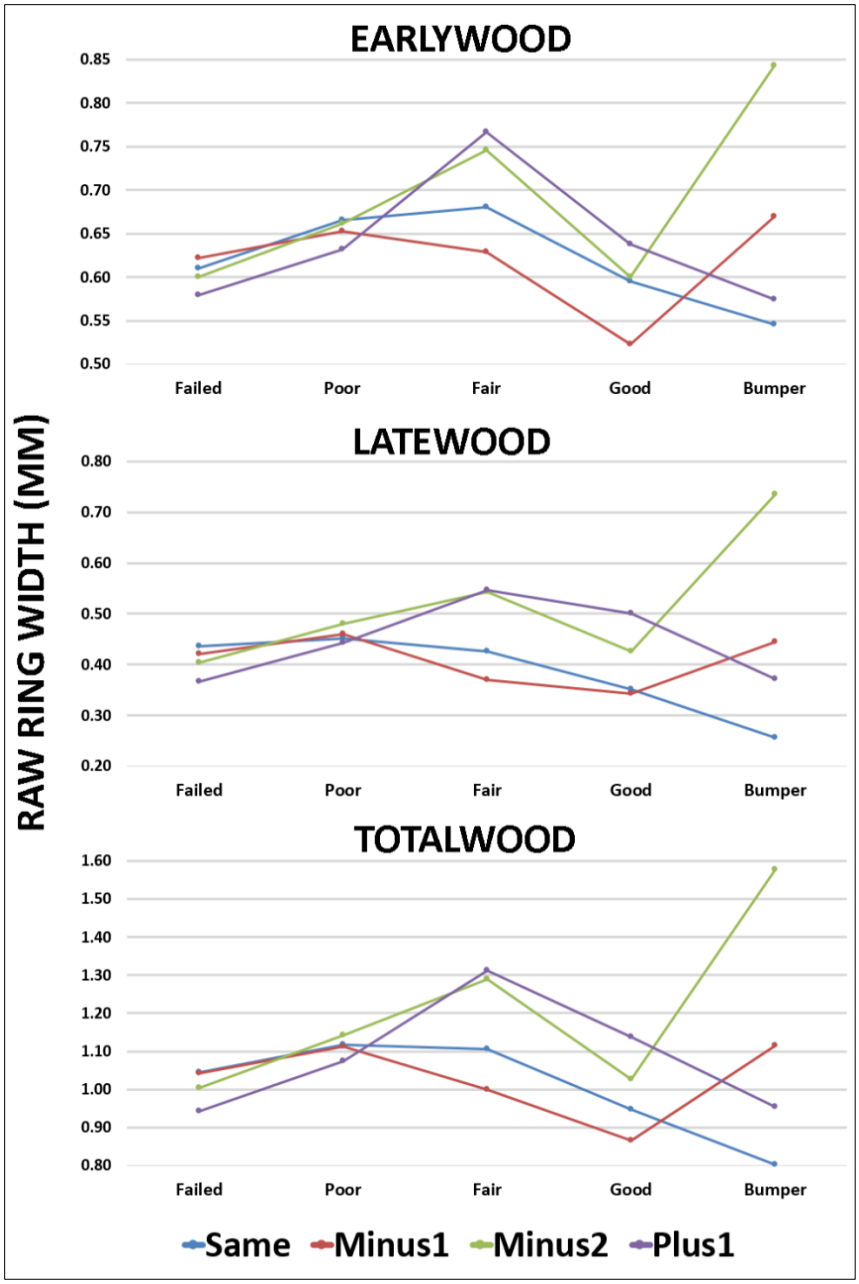

Figure 3.4. Mean Ring Width When Grouped By USFS Cone-Crop Classes. Cone Crop Classes Are Defined By The USFS As Follows Failed (0–9), Poor (10–24), Fair (25–49), Good (50–99), And Bumper (≥ 100).

Mean sensitivity expressed no correlation with individual cone contribution (Figure 3.5). I preformed this analysis using all trees (n = 63) expecting some relationship between trees with more sensitivity and their cone contribution. Instead, I found an even distribution of data points with no clear trend.

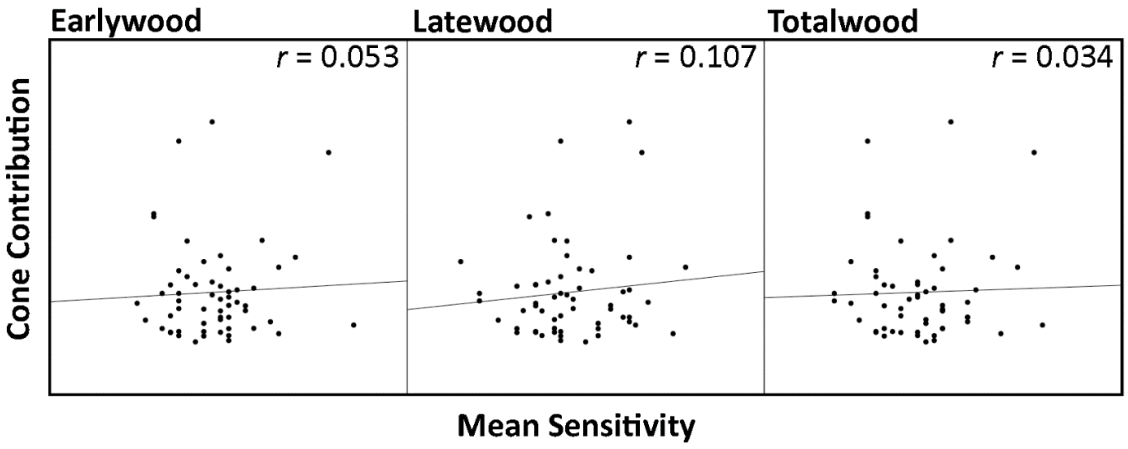

Figure 3.5. Correlation Coefficients Between Mean Sensitivity And Cone Contribution. All Correlations Are Not Significant ($P > 0.05$). N = 63

I developed indexed ring-width chronologies for all sites for regression analysis. Table 3.6 provides R^2 statistics from the regression analysis for all sites and ring-width measurements. The two Eglin AFB sites explained considerably more variance in averaged PDSI relative to the other four sites. Coincidently these two sites had the lowest averaged cone production of 15.34 cones per year as opposed to the other four sites that varied between 24.4–28.9 cones per year on average. The inclusion of cone data in each regression model marginally improved explainable variance in averaged PDSI, and never improved R^2 values by more than 3%. Average ring width varied between sites but did not appear to be

related to PDSI or number of cones produced. Last, individual trees that were significantly correlated with climate were not significantly correlated with cone production ($p > 0.05$).

Table 3.6. Results From The Regression Analysis. Sites Are Ordered Left To Right In The Table From Least Cones Produced To Most Cones Produced. Numeric Values Indicate R^2 Values When Using Only PDSI Or PDSI And Cones As Predictors Of Ring Width. Average Widths Are Raw-Ring Width Values (Mm). All Models Were Significant ($P < 0.05$) Unless Noted With The Subscript Ns. TW = Totalwood, LW = Latewood, EW = Earlywood

	Boondocks	Rattlesnake	Blackwater	Jones	Croker	Farm Forty
			TW			
Avg. cones	15.3	15.3	24.4	27.8	28.9	28.9
Avg. width	2.16	1.66	2.49	2.15	2.16	2.00
PDSI	0.405	0.31	0.064_{ns}	0.027_{ns}	0.125	0.072
PDSI Cones	0.423	0.322	0.098_{ns}	0.043_{ns}	0.141	0.091_{ns}
			LW			
Avg. cones	15.34	15.34	24.43	27.83	28.9	28.9
Avg. width	1.02	.76	1.21	.96	1.06	1.00
PDSI	0.404	0.361	0.15	0.106	0.157	0.087
PDSI Cones	0.411	0.369	0.168	0.11_{ns}	0.163	0.099_{ns}
			EW			
Avg. cones	15.34	15.34	24.43	27.83	28.9	28.9
Avg. width	1.14	.90	1.29	1.20	1.10	1.00
PDSI	0.282	0.29	0.024_{ns}	0.011_{ns}	0.006_{ns}	0_{ns}
PDSI Cones	0.291	0.303	0.045_{ns}	0.011_{ns}	0.028_{ns}	0.023_{ns}

3.5 Discussion

My research is the first analysis using longleaf pine individual cone data paired tree-ring width from the actual trees used in the multi-decadal research study. Access to the individual cone data provided useful information into the variability of cones produced

within each site. I showed the number of cones produced between trees within a site varies considerably, yet this variation is collapsed when only site averages are disseminated by the USFS. In some extreme cases, one tree produced over 500 cones in one year. For example, one tree at Jones produced 854 cones in 2014. This accounted for 58% of all cones produced between the 12 trees at Jones. By comparison the next most cone producing tree at Jones that year produced 16% of the total cone crop, and the remaining ten trees contributed from six to less than one percent of the year's total. It is important to note that for other years the differences are less extreme, yet the overall contribution of each tree to the total of all cones produced is right skewed and not equitable within a site (Figure 3.3). The disproportionate nature of cone production between trees and years conflicts classifying longleaf pine as a masting species. Masting species synchronously produce seed crops at the population level (Kelly 1994, Isagi *et al.* 1997, Koenig and Knops 2005) therefore one individual producing a large seed crop while others fail to produce does not fit this contemporary definition. I did not test the number of years where cone contribution is more equitable relative to years where one tree produces the majority of cones. Similarly, it is important to note that the data I used are from small sample sizes (10–12 trees) therefore caution must be taken in interpreting my results. That said, numerous of studies use these data e.g. (Boyer 1979, 1987, 1998, Pederson *et al.* 1999, Chen *et al.* 2016a, Chen *et al.* 2016b, Guo *et al.* 2016) to understand masting processes and they exclusively use the averaged values reported by the USFS. I did not isolate "super producing" trees to understand their masting/ring-width relationships, yet future studies could investigate their characteristics and

the intrasite variability of longleaf pine masting using more data than the ten trees in the long-term study.

Trees in my study were young relative to the maximum age (> 450 years) that longleaf pine can live (Earle 2017). All sites where longleaf pine cones are counted are second growth and part of an ongoing research project initiated in the late 1950's (Connor *et al.* 2014). I found that average tree age never exceeded 100 years. Therefore, inference regarding longleaf pine masting pertains to second growth stands. I did not test cone production between age groups within a stand as trees in this study did not vary in age by more than 10 years. Future research should address cone production in old-growth (> 200 years) stands to assess how these trees produce mast relative to their younger counterparts.

As expected from previous literature (Henderson and Grissino-Mayer 2009, Knapp *et al.* 2016), latewood mean sensitivity values were highest indicating variability of environmental conditions (e.g. climate or masting) modulates ring growth later in the growing season. Longleaf pine cones develop over a two-year process (Brockway *et al.* 2006) where during the final year, the year of cone count, the cones expands in size from 2.5 cm to 18 cm by June (Boyer 1990). Cones continue to mature and will range in size 10–25 cm by mid-October when they finally release their seeds. I expected to find more significant correlations between cones and earlywood and totalwood ring widths as the majority of cone growth takes place earlier in the growing season. I did not find strong distinctions between these ring width measurements (Table 3.3). Earlywood ring widths displayed a significant "hangover effect" whereas latewood did not. There were also instances where latewood ring width/cone correlations were stronger than for earlywood. At present, only totalwood

widths have been reported in previous *dendromastecology* studies (Speer 2001, Drobyshev *et al.* 2010, Drobyshev *et al.* 2014, Hacket-Pain *et al.* 2015), therefore my research helps determine when during the growing season reproduction is more likely to be recorded in growth rings. While timing of latewood initiation was not tested, perhaps the greatest strain of resources via cone production in longleaf pine takes place during the phase of earlywood growth yet is somehow carried over and imprinted in latewood growth later in the growing season.

I provided evidence that corroborates with Woodward *et al.* (1994) indicating above-average mast years coincide more frequently with narrower growth rings. My data show that the narrowest growth rings, smaller than one standard deviation from the mean, are nearly twice as likely to occur during years when there are higher than average cones produced (Table 3.4). When I classified ring width and the number of cones produced using the USFS cone-class sizes (Table 3.5, Figure 3.4) I found that the cones in largest class (bumper, ≥ 100 cones) coincided with ring widths that were significantly different from other cone-crop classes. For same-year comparisons these ring widths were the narrowest and for the 2-year lag relationship they were the largest. I believe these bumper cone crops are the most influential at depleting internal resources of the trees during their final year of their 2-year life cycle. This is also the year when cones expand in size from 2.5 to 18 cm in length (Boyer 1990). Cones crops < 100 cones per tree do not have the same effect on influencing radial growth of the same year as mean ring width between these cone classes were not significantly different from one another. These results differ from my previous findings (Chapter 2, Patterson and Knapp 2016b) that indicated the strongest relationships existed when cones were lagged one year from radial growth. Perhaps my previous findings were

due to differences in sampling and data standardization. I confirmed with Dr. Dale Brockway that no changes in management have occurred at the six sites during the years where available cone data existed. I tested the relationship between cones and mean sensitivity and found no significant association. It is only during bumper years where internal resources are drained, and I have shown from the individual tree data that these years are infrequent (Figure 3.3). Therefore, most of the signal between cones and ring width is lost when ring widths and cones are averaged at the stand level and may only come into play when all trees produce large cone crops (i.e. productive sites and bumper years). I believe the 2-year lag relationship between cones and ring width is related to climatic conditions. The greatest Catkin (female strobili) and conelet (male strobili) development occurs during years with abundant rainfall throughout the growing season. Not surprisingly, abundant rainfall is positively correlated with radial growth of longleaf pine (Devall *et al.* 1991, Henderson and Grissino-Mayer 2009, Patterson *et al.* 2016). Therefore, the positive relationship between radial growth rings two years prior to cone crop is likely corroborated with rainfall throughout the growing season.

My regression models indicated mast was a weak predictor for explainable variance in average PDSI and does not warrant further investigation. Similarly, I did not find a relationship between trees that individually correlated with climate and their cone production. I found the most explainable variance in average PDSI were for the two Eglin AFB sites (Boondocks and Rattlesnake), that happened to have the lowest average cone production of the six sites examined. At Boondocks, total ring-width alone explained 40.5% of the variance in July–September PDSI. Taking the square root of this value, indicative of

its correlation with climate, results in a strong, significant correlation $r = 0.64$, $p < 0.001$. This value is markedly higher than any previous tree-ring/climate correlation with PDSI from Eglin AFB, with Henderson and Grissino-Mayer (2009) reporting *r*-values of totalwood and monthly PDSI in the range of 0.3—0.4. I have to distinguish my findings from this previous research as I only examined these correlations for years of available averaged cone data ca. 1968–2015 with the omission of 1988–1993 where data were unavailable. Therefore I examined climate/growth relationships with PDSI for only 42 years as opposed to 108 years reported by Henderson and Grissino Mayer (2009). Many of my regression models were not significant, but when they were the inclusion of the mast variable never improved explainable variance by more than 1.8%. This weak improvement in variance explained indicates the pairing of mast with radial growth would unlikely improve the strength of a climate reconstruction. I did not evaluate instances where mast years overlap drought years leading to a potential secondary effect of reducing radial growth, as cautioned in Hacket-Pain *et al.* (2015). As only bumper years significantly reduce radial growth, and with these years occurring so infrequently, I deemed this exercise unnecessary. Additionally, I did not isolate "super producing" trees into a separate chronology for regression analysis as too few existed in each stand.

It should be noted that the strongest relationships between radial growth and mast were for the lowest cone-production sites at Eglin AFB. I believe that few larger cone years at these sites means less of a chance for bumper crops (≥ 100 cones per tree) to modulate growth rings and thus alter relationships between radial growth and climate. The same holds true at the most productive sites that produced almost twice the number of cones on average

and had the weakest relationships with PDSI. It may be advisable when seeking stands for dendroclimate analysis to choose those with the fewest cones as I have shown that: 1) individual trees that produce bumper crops on a given year (≥ 100 cones per tree) have significantly narrower mean ring width and 2) sites with more cones have weaker climate/growth relationships. Therefore, due to the infrequency of bumper crops between years or even between trees within a stand, I believe selecting sites with fewer cones is advisable rather than individually selecting trees in each stand with the fewest cones. Even if one or two trees in a low producing stand is a major cone producer, its inclusion in a master chronology would not likely alter the stand-level climate analysis. However, when comparing a low-production site from one with higher cone production the results seem indicate the tradeoff of mast and ring width alters climate relationships significantly.

3.6 Conclusion

My study examined longleaf pine masting and radial growth relationships at the individual tree level. Mast data from each tree revealed that the production of cones is not equitable. Despite a disproportionate mast production between trees there was an overall negative relationship between cone production and radial growth. I was able to show where the narrowest growth rings were associated with greater than average mast, and similarly how the largest masting events were associated with statistically-significant reduced growth. When mast data were incorporated into linear models used to explain variations in PDSI their inclusion was inconsequential. I believe that due to the infrequency of bumper mast years, longleaf pine cones only rarely alter growth rings at the individual tree level. Therefore,

climate reconstructions that use longleaf pine are likely not influenced by masting, and low growth values are more attributable to external factors rather than reproductive strain.

My research used individual cone counts from the USFS. Their protocol for counting cones has been used for nearly sixty years and despite technological advancements remains the same for sake of data continuity. I believe that counting cones for more than 10–12 trees per stand could contextualize that variability of the limited sample size in each stand. The use of cameras and drones could expedite this process and future research could compare a new count method to traditional techniques. Similarly, this research is based on whole cone counts yet no information is available regarding the number, size, and variation of the seeds that are contained within each pine cone. In addition there is no information about variation in cone size within or between trees during productive cone years. As energy and nutrients are expended in the production of cones and seeds, information is needed to determine whether there is a resource drain in radial growth during particularly seed-rich years or years where cones are particularly large. Perhaps future cone count methods can examine the total number of cones produced and also the variation in size and quantity of seeds per cone.

CHAPTER IV

LONGLEAF PINE MASTING, NORTHERN BOBWHITE QUAIL, AND TICK-BORNE DISEASES IN THE SOUTHEASTERN UNITED STATES

This chapter was prepared for submission to the *Annals of the American Association of Geographers*. The use of "we" and "our" refers to Dr. Paul Knapp and myself who co-authored the manuscript.

4.1 Abstract

The relationship between oak mast and Lyme disease incidence in humans is established in the Northeastern U.S. yet mast-disease relationships have not been explored in the southeastern U.S where a multi-decadal dataset exists for longleaf pine mast. Here, we examine if a relationship exists between longleaf pine mast and tick borne incidence in humans using climate, wildfire, and bird count data as possible influential variables. We examined the relationship between longleaf pine mast data and tick-borne disease incidence for Lyme, Spotted Fever Group Rickettsia (SFGR), and *Ehrlichia chaffeensis* (ehrlichiosis) using one-sided person correlations at ten individual masting locations and for the entire masting region in the southeastern U.S. Both mast and disease data were correlated with Audubon Society Christmas bird counts for northern bobwhite quail (*Colinus virginianus)*, Palmer Drought Severity Index data, and fire occurrence data at the ten individual masting

locations and for the entire region. Region-wide mast from the previous year were positively correlated with northern bobwhite quail and negatively correlated with Lyme disease. Additionally, northern bobwhite quail were negatively correlated with SFGR and ehrlichiosis, and both drought severity and fire were not correlated with the other variables. We posit the nutrient-rich pine seeds become available in late autumn and positively influences northern bobwhite quail populations the following year. As quail diet transitions from seeds in cool months to ground-dwelling insects the following spring and summer, we hypothesize their ability to consume ticks impacts their populations to significantly reduce disease incidence in humans.

4.2 Introduction

Longleaf pine (*Pinus palustris* Mill.) is native to the southeastern United States and exists primarily within the Coastal Plain and Piedmont physiographic regions, yet outlier populations are dispersed in the Ridge and Valley region of Northern Alabama and Georgia (Peet 2006) and the Uwharrie Mountains of central North Carolina (Patterson and Knapp 2016a). Once considered the dominant coastal-plain pine tree prior to European settlement (Ware *et al.* 1993), only a fraction of its range remains intact due to centuries of land-use changes including deforestation, fire suppression, conversion of forest savanna to agriculture, and the naval stores industry (Frost 1993). Recent analysis (Oswalt *et al.* 2012) documenting the extent of longleaf pine forests in the southeastern U.S. estimates that approximately three percent of the original forests remain, with a range reduction from 38 million hectares to just over one million hectares. The extant stands of longleaf pine support a suite of rare and endemic species (Means 2006), with remnant longleaf savannas harboring

exceptionally high plant diversity for the Western Hemisphere (Peet and Allard 1993). Thus, the rarity and importance of longleaf pine forests has promoted research devoted to better understanding longleaf pine forest reforestation and how interannual mast (i.e., cone crop) variability affects regeneration success.

Annual cone production for longleaf pine is variable due to episodic cone masting cycles (Boyer and Peterson 1983). Above-average cone crops occur throughout the species' range every 5–7 years (Wahlenberg 1946), with large "bumper" crops occurring every 8–10 years (Maki 1952). In an effort to better understand masting cycles of longleaf pine, annual cone-count inventories were initiated by W.D. Boyer of the United States Forest Service (USFS) in Escambia County, Alabama in 1958 and have been expanded to over 10 locations throughout the southeastern US through 2016 (Connor *et al.* 2014, Brockway 2015). Spatiotemporal variability of cone mast has been observed throughout the species' range that is attributable to either changes in forest management or climate conditions leading to improved pollination efficiency and conelet survival (Croker and Boyer 1975, Boyer 1987, 1997, 1998). Additionally, others (Shoulders 1967, Pederson *et al.* 1999, Leduc *et al.* 2015, Chen *et al.* 2016a, Guo *et al.* 2016) have found a suite of monthly climate conditions that correlate with longleaf pine mast during its 3-year development. Bumper mast years are critical for successful longleaf pine regeneration (Brockway *et al.* 2006) and for providing food resources for a number of species native to longleaf pine forests (Means 2006). Studies using the USFS mast data either have principally observed environmental factors that influence mast including thinning (Boyer 1979), climate (Pederson *et al.* 1999, Guo *et al.* 2016, Leduc *et al.* 2016), or the inherently complex and sporadic nature of mast variability

(Chen *et al.* 2016a). To our knowledge, these data have not been used to address potential interactions between mast abundance and endemic bird populations and how these relationships may indirectly affect the incidence of tick-borne disease prevalence in humans.

Over two decades of research has linked masting cycles of hardwood trees (*Quercus* spp.) to mast predator populations (deer, mice, chipmunk), which serve as hosts for a variety of ticks that can transmit tick-borne diseases to humans. The majority of the mast-tick-disease research has focused on the northeastern US region due to the density of reported cases of Lyme disease and the geographic dispersal of *Ixodes dammini* Say, the blacklegged/dog tick that can spread *Borrelia burgdorferi* Johnson, the spirochete bacteria causing Lyme disease in humans. Ostfeld *et al.* (1995) observed an unusual increase in larval ticks in oak forests the year following a bumper acorn mast positing that white-tailed deer (*Odocoileus virginianus* Zimmermann) feeding on the bumper mast harbored adult ticks that would drop off and lay their eggs the following spring. Subsequent studies tested the theory of an 'acorn connection' (Ostfeld 1997) to explain how mast variability of hardwood trees modulates host populations that in turn affect tick populations and alter the propensity to spread Lyme disease to humans (Jones *et al.* 1998, Ostfeld *et al.* 2001, Schauber *et al.* 2005, Ostfeld *et al.* 2006b) These studies have shown that acorns of year X positively influences mast consumer populations in year X+1 that positively influences infected tick nymph abundance and Lyme disease incidence in year X+2. Here, we address if a similar relationship exists between longleaf pine mast, the endemic northern bobwhite quail (*Colinus virginianus* Linnaeus) and tick-borne diseases in the southeastern U.S.

In the southeastern U.S., several tick species carry bacteria associated with a variety of tick-borne diseases (Stromdahl and Hickling 2012). The Gulf Coast Tick (*Amblyomma maculatum* Koch) shares a range similar to that of longleaf pine and is the principal carrier of *Rickettsia rickettsia,* the agent for Rocky Mountain spotted fever (RMSF) (Parola *et al.* 2013, Paddock and Goddard 2015). Other southeastern U.S. tick species include the Lonestar (*Amblyomma americanum* Linnaeus), American Dog (*Dermacentor variabilis* Say), Brown Dog (*Rhipicephalus sanguineus* Latreille), and Blacklegged (*Ixodes scapularis* Say) ticks. These species can transmit bacteria to humans and include multiple species of Rickettsia attributed to spotted-fever group rickettsiae (SFGR), *Ehrlichia chaffeensis* (ehrlichiosis), and *Borrelia burgdorferi* (Lyme disease) (Childs and Paddock 2003, Stromdahl and Hickling 2012, Nadolny *et al.* 2014). Both SFGR and ehrlichiosis have not been studied for mast–disease relationships yet are of growing human-health concern in the southeastern U.S. (Parola *et al.* 2013) and pathogens such as *Rickettsia parkeri* that comprise SFGR can be found in >50% of gulf-coast ticks (Nadolny *et al.* 2014). Similarly, ehrlichiosis, whose primary vector is the Lone Star tick (Varela-Stokes 2007, Goddard and Varela-Stokes 2009), is most prevalent in the Southeast and south-central U.S. (CDC 2016).

The principal method for reducing tick populations in longleaf pine forests has inadvertently occurred through prescribed burning (Hoch *et al.* 1972, Mather *et al.* 1993, Gleim *et al.* 2014). Gleim *et al.* (2014) found a significant reduction in four species of ticks associated with long-term prescribed burning at the J.W. Jones Ecological Research Center (and USFS mast-count site) that they deemed consistent with previous research regarding the influence of fire in pine and mixed-pine forests (Jacobson and Hurst 1979, Cully 1999).

Similarly, biological control through the use of fungicides (Ostfeld *et al.* 2006a) or bird species (Ostfeld and Lewis 1999) has provided mixed results. Anecdotal evidence exists for the ability for northern bobwhite quail, a specialist to longleaf pine forests (Means 2006), to consume and thus reduce tick populations, but no studies have documented if this activity affects the incidence rate of registered tick-borne diseases in humans. Likewise, longleaf pine literature does not include discussion on the effects of masting cycles on tick-borne disease prevalence in the southeastern U.S.. In this study we examine the relationship between mast, tick-borne disease incidence and bird species endemic to longleaf pine using a multidecadal longleaf pine mast dataset. Specifically, our goals are to: 1) investigate the association between longleaf pine mast and tick-borne illness; 2) examine potential cofounding variables including bird species counts, climate data, and area burned; and, 3) discuss geographic variations that elucidate disease ecology in longleaf pine forests.

4.3 Materials and Methods

4.3.1 Pine-Cone Data

Longleaf pine cone mast is counted annually each April at 11 sites in the longleaf pine range from eastern North Carolina to central Louisiana and reported by the USFS (Brockway 2015). Mast counts for each site represent the cones that will ripen and release seeds during October–November following the spring survey. Based on mast-data completeness, we selected 10 locations (Figure 4.1, Table 4.1) excluding one site, Ordway-Swisher Biological Station, as 2015 was its first year of data collection. For each location, we used all available years coinciding with tick-borne disease data availability unless data were otherwise unavailable (Table 4.1).

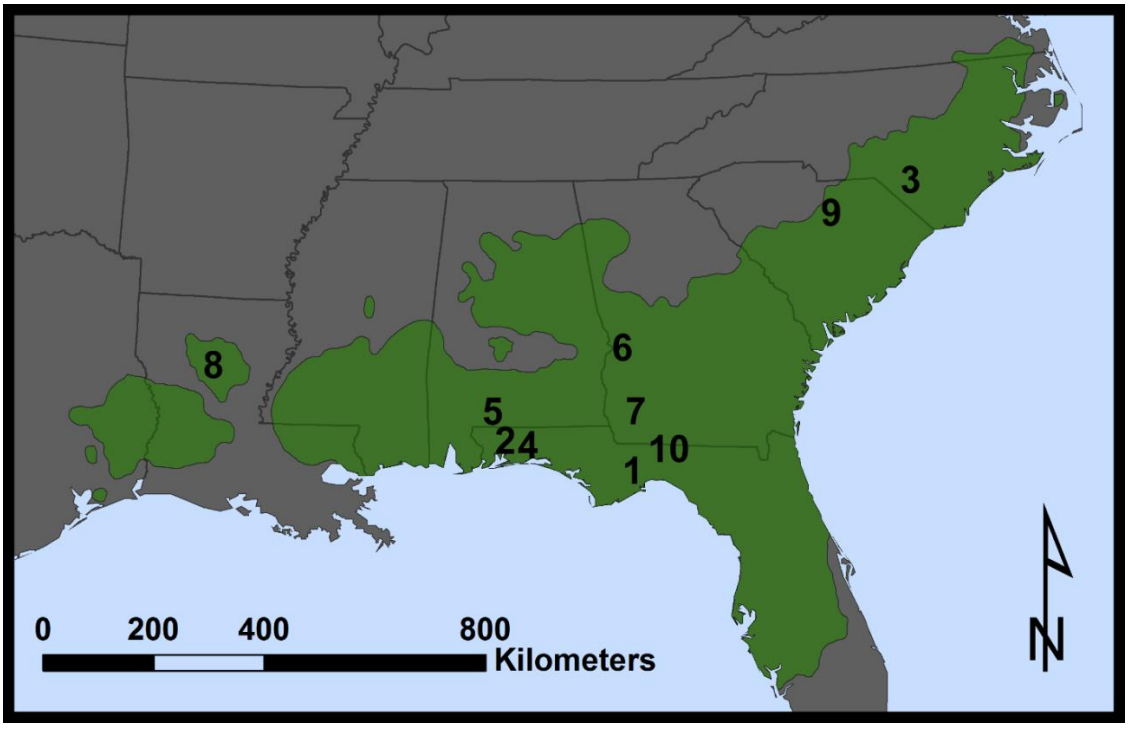

Figure 4.1. Location Of The 10 USFS Cone Collection Sites Numbered Alphabetically As Listed In Table 4.1 Within The Historic Longleaf Pine Range (Green).

Table 4.1. Location And Range Of Masting Years At USFS Cone-Count Locations. Sites Marked With An * Have Truncated Mast Dataset From The Full 22-Year Range (1993–2014) Used In The Analysis.

Cone-measuring location	Years of available data
Apalachicola National Forest, Leon County, FL	1966-1974, 1976–1978, 1992–2015
Blackwater River State Forest, Santa Rose County, FL	1967–2015
Bladen Lake State Forest, Bladen County, NC	1968–1974, 1977–1979, 1991–2015
Eglin Air Force Base, Okaloosa County, FL*	1968-1987, 1994–2015
Escambia Experimental Research Forest, Escambia County, AL	1958–2015
Fort Benning Military Base, Chattahoochee County, GA*	1993, 1995–2005, 2007–2015
Jones Ecological Research Center, Baker County, GA	1967–2015
Kisatchie National Forest, Grant County, LA	1967–1974, 1977–2015
Sandhills State Forest, Chesterfield County, SC	1969–2015
Tall Timbers Research Station, Leon County, FL*	1999–2015

4.3.2 Disease Data

Annual, county-level tick-borne disease incidence data were obtained from the US Centers for Disease Control and Prevention (CDC) for Lyme, SFGR, and ehrlichiosis. Lyme data were downloaded from the CDC Lyme webpage whereas a data request was fulfilled through the National Notifiable Disease Surveillance System (NNDSS) for SFGR and ehrlichiosis. SFGR is a composite of three bacteria/tick species including *Rickettsia rickettsia* carried by three tick species including the American dog tick, Rocky Mountain wood tick *(Dermacentor andersoni),* and the Brown dog tick*; Rickettsia parkeri* carried by the Gulf Coast tick (*Amblyomma maculatum*); and *Rickettsia* species 364D carried by Pacific Coast tick (*Dermacentor occidentalis*). Similarly, ehrlichiosis describes three bacterial diseases and we were able to obtain confirmed cases caused by the species *Ehrlichia chaffeensis*, which is most commonly carried by the Lone Star tick. The NNDSS compiles confirmed reports from each US county, state, territory, and/or reporting jurisdiction and thus incidence data may be subject to local variations from heterogeneous surveying and reporting standards. County-level incidence for the three diseases were available for 22 years (1993–2014) for SFGR and 15 years (2000–2014) for Lyme and ehrlichiosis.

4.3.3 Climate-Data

Climate-masting research examining climate variables that influence longleaf pine mast (Pederson *et al.* 1999, Leduc *et al.* 2015) suggest Palmer Drought Severity Index (PDSI) conditions during the previous October–April of year two of cone development are most critical. To test if this relationship was operative at our 10 sites during our study period, we

averaged October–April monthly PDSI data obtained from the National Climate Data Center (NCDC 2016) for 1992–2014 for all climate divisions corresponding with each cone measurement site, which included Climate divisions AL7, FL1, GA4, GA7, LA5, NC6, and SC3.

4.3.4 Fire Data

ArcGIS Shapefiles for fire occurrence were obtained from the Federal Fire Occurrence Website (Goldman 2016). The fire occurrence data consist of fire records by location and acreage burned on all federal lands. Participating federal agencies include the Bureau of Indian Affairs, Bureau of Reclamation. Bureau of Land Management, U.S. Fish and Wildlife Service, National Park Service, and the U.S. Forest Service. Data were downloaded for all fires 1980–2014. We used geographic location (X,Y coordinates) and total acreage burned for all fires on federally managed lands.

4.3.5 Bird Data

We used the Audubon Society's Annual Christmas Bird Count (CBC) for state-level bird census data (National Audubon Society 2016). CBC counts consist of 10+ bird watchers surveying all bird species and numbers within a defined 24 km diameter circle at multiple sites throughout a state (Bock and Root 1981). For use of analysis, the number of birds for each species reported is divided by the number of party hours from the multiple data observation sites to provide a standardized value (Bock and Root 1981). Standardized (bird number/party hour) bird data during 1993–2014 were downloaded for five bird species that are either specialists or endemics to longleaf pine ecosystems (Means 2006), including

the red-cockaded woodpecker (*Leuconotopicus borealis* Vieillot), northern bobwhite quail, white-breasted nuthatch (*Sitta carolinensis* Latham), brown-headed nuthatch (*Sitta pusilla* Latham), and Bachman's sparrow (*Aimophila aestivalis* Lichtenstein). CBC data for the five bird species were acquired for the six states with longleaf pine mast sites.

4.3.6 Data Analyses

Mast relationships with disease, CBC, fire, and PDSI were analyzed at both region-wide (i.e., mean of 10 mast sites) and site-based scales. Mast-count locations, all diseases (by county) and fire data (X,Y coordinates) were entered into ArcGIS 10.2.2 (ESRI 2013). State-level CBC and climate-division level PDSI were manually selected for analysis. We tested for the strongest correlations between mast and disease data based on radiating distances from the mast-site's county border (ArcGIS) and selected 25km radii for all analysis. Thus, we selected all counties intersecting a 25 km radius from each mast site's county to create 10 aggregate groups each representing the total annual tick-borne cases for each disease associated with each mast site. The same 25-km radius was used to select all fires within a distance from each cone-count county.

For regional analysis we summed disease data for all 10 mast site aggregate groups to create a regional annual, total for each of the three diseases. We used the CBC search portal to retrieve standardized bird counts for the five bird species averaged across the six states the mast-count sites were located. We also summed the annual area burned for all fires with a 25-km radius from the masting sites to create an annual, regional summary for fire. We correlated the region-wide (i.e., all sites) mean cone mast with the total number of cases for each disease, bird count, and area burned using one-tailed Pearson product-moment

correlations for current, lag-one, and lag-two years as others (Jones *et al.* 1998, Schauber *et al.* 2005, Ostfeld *et al.* 2006b) have found lagged relationships between acorn mast and disease incidence. For example, we tested the relationship between region-wide mast of 2012 with bird populations and tick-borne illness of 2012 (current), 2013 (lag one), and 2014 (lag two).

For site-based analysis we tested each masting site's annual mast with its aggregate county cluster of the three diseases. Similarly, mast from each site was correlated with CBC data from the state of mast-site residence. We also tested the relationship between disease prevalence from each aggregate county cluster with CBC data from the corresponding state of mast-site residence. For each mast site we correlated annual mast and tick-borne disease incidence with drought severity data from the residing climate division. CBC data were correlated against PDSI for the six climate divisions. We tested the site-based relationships using one-sided Pearson product-moment correlations for current year and one- and two-year lags. Fire data were incomplete for all years at each site thus were used in grouped analysis only.

4.4 Results

4.4.1 Regional

Current-year cone mast was not significantly correlated with bird, disease, or fire variables, yet mast of the previous year was correlated with current-year bird and disease data. Northern bobwhite quail populations were positively correlated (r =0.364, p = 0.048, n = 22) with average longleaf pine mast of the previous year indicating that larger seed crop years in year X coincided with increased quail CBC counts in year X+1. No other

specialist/endemic bird species had significant positive correlations with mast and were thus excluded from further analysis. Average longleaf pine cone mast of the previous year was negatively correlated with Lyme disease (r = -0.54, p = 0.018, n = 15) but not with SFGR or ehrlichiosis. Northern bobwhite quail were negatively correlated with SFGR (r = -0.71, p < 0.001, n=22) and ehrlichiosis (r = -0.68, p = 0.003, n = 15) of the same year. Area burned was not significantly correlated with mast, disease or CBC data for current or lagged relationships.

4.4.2 Site-Specific Results

Site specific analysis cross-correlated mast from the 10 masting sites, three diseases per sites, quail data for six states, and averaged October–April PDSI for seven climate divisions with significant values (Tables 4.2–4.4) occurring at all sites. Longleaf pine mast of the previous year was positively correlated with northern bobwhite quail only at Apalachicola (r = 0.42 p = 0.03 n=22). The relationship was consistently positive but not statistically significant for another seven of the 10 sites. Longleaf pine mast crops of the previous year were consistently and negatively correlated with Lyme (Bladen, Tall Timbers, Apalachicola, and Eglin) and SFGR (Sandhills, Blackwater, Eglin, and Escambia), but not for ehrlichiosis (Table 4.2). Northern bobwhite quail was negatively correlated with SFGR at Ft. Benning, Blackwater, and Escambia, but responses for Lyme and ehrlichiosis were inconsistent among sites (Table 4.3). Average October–April PDSI did not correlate with mast at any site, yet was positively correlated with northern bobwhite quail at six sites including Apalachicola, Blackwater, Eglin, Tall Timbers (r = 0.43, p = 0.03, n=22; first four from same climate division), Kisatchie (r = 0.45, p = 0.02, n=22), and Sandhills (r = 0.54, p < 0.01, n=22).

Average October–April PDSI was negatively correlated with Lyme at Sandhills (r = -0.48, p = 0.04, n=15) and SFGR at the neighboring Florida sites Backwater (r = -0.4, p = 0.03, n=22) and Eglin (r = -0.4, p = 0.03, n=20) (Table 4.4).

Table 4.2. Significant ($P \leq 0.05$) Pearson Product-Moment Correlations Between Mast And Disease Variables By Site.

Site	**Lyme**	**SFGR**	**Ehrlichiosis**
Apalachicola	r = -0.44, p = 0.05, n=15		
Blackwater		r = -0.4, p = 0.03, n=22	
Bladen	r = -0.44, p = 0.05, n=15		
Eglin	r = -0.48, p = 0.04, n=15	r = -0.39, p = 0.05, n=20	
Escambia		r = -0.36, p = 0.05, n=22	
Ft. Benning			
Jones			
Kisatchie			
Sandhills		r = -0.49, p = 0.01, n=22	
Tall Timbers	r = -0.58, p = 0.01, n=15		r = -0.6, p = 0.01, n=15

Table 4.3. Significant ($P \leq 0.05$) Pearson Product-Moment Correlations Between Quail And Disease Variables By Site.

Site	**Lyme**	**SFGR**	**Ehrlichiosis**
Apalachicola			
Blackwater		r = -0.58, p < 0.01, n=22	
Bladen			r = -0.55, p = 0.02, n=15
Eglin			

Escambia		r = -0.68, p < 0.01, n=22	
Ft. Benning		r = -0.41, p = 0.03, n=22	
Jones	r = -0.58, p = 0.02, n=15		
Kisatchie			
Sandhills			
Tall Timbers	r = 0.52, p = 0.02, n=15		r = 0.44, p = 0.05, n=15

Table 4.4. Significant ($P \leq 0.05$) Pearson Product-Moment Correlations Between Average October–April PDSI And Mast, Quail, And Disease Variables By Site.

Site	**Cone**	**Northern Bobwhite Quail**	**Disease**
Apalachicola		r = 0.43, p = 0.024, n=22	
Blackwater		Same as Apalachicola	SFG*R* r = -0.4, p = 0.03, n=22
Bladen			
Eglin		Same as Apalachicola	SFG*R* r = -0.4, p = 0.03, n=20
Escambia			
Ft Benning			
Jones			
Kisatchie		r = 0.45, p = 0.02, n=22	
Sandhills		r = 0.54, p < 0.01, n=22	Lyme r = -0.48, p = 0.04, n=15
Tall Timbers		Same as Apalachicola	

4.5 Discussion

Our study is the first to analyze a multi-decadal relationship between northern bobwhite quail and longleaf pine mast. Our data suggest that the nutrient-rich seeds from longleaf pine mast become available in the fall and winter and positively influence northern bobwhite quail populations. Based on data from five locations in the longleaf pine range,

Reid and Goodrum (1979) found longleaf pine seeds comprised 85% of northern bobwhite quail diet during peak seed availability in November and 22–46% of the total winter diet. Conversely, during a mast failure event, longleaf pine seeds comprised 15% of the November diet (Reid and Goodrum 1979). We found that longleaf pine mast relationships were strongest when bird and disease variables were lagged one year; findings consistent with studies that have examined relationships between white-footed mice (*Peromyscus leucopus* Rafinesque; Ostfeld *et al.* 2001) and chipmunk (*Tamias striatus* Linnaeus; Wolff 1996) populations and acorn mast. Thus, we posit masting years provide ample food stores to improve quail breeding success the following spring and ultimately larger quail populations recorded by CBC volunteers one year following mast.

Fluctuating bobwhite quail populations may impact tick populations. Northern bobwhite quail feeding choice transitions from principally longleaf pine mast during the cool season to a diet with higher proportions of ground dwelling insects, particularly for chicks and adult females (Eubanks and Dimmick 1974; Brennan and Hurst 1995), during spring and summer that may include tick consumption. Thus, the negative correlation between longleaf pine mast and reported tick-borne disease incidence may be driven by a series of sequential events: 1) increased mast leads to increased northern bobwhite quail populations; 2) increased quail populations increase the number of spring fledglings; 3) tick populations decrease via heavy feeding by fledglings in the spring and summer months; and 4) tick-borne disease incidence decreases because of lowered tick-human interactions. This series of events may be particularly operative for SFGR, which represents the highest incidence rate of tick-borne illness in the southeastern U.S..

Mast was correlated with quail population regionally, but only with a single location when examined at site level. This latter, less-robust association likely reflects smaller sample size at individual sites. At nearly all sites, however, the correlation was directionally consistent, which helps to explain why mast is positively correlated with northern bobwhite quail when averaged across sites, but only with Apalachicola when tested individually. Other factors including climate and fire may modulate bird populations and tick-borne disease prevalence independently, yet the linkages remain poorly understood. In the northeastern U.S., Subak (2003) found a positive relationship between Lyme disease and two-year lagged June PHDI while Schauber *et al.* (2005) found a negative relationship between one-year lagged summer precipitation and Lyme incidence. Likewise, we found the most important climate variable that affects longleaf pine mast (October–April PDSI) had few consistent effects on any of our disease variables. The only consistent climate relationship were positive correlations between PDSI and northern bobwhite quail where positive PSDI values indicate wetter winter and spring soil-moisture conditions that presumably benefit quail populations the following year. This finding supports Lusk *et al.* (2001) who found winter precipitation positively affected northern bobwhite quail populations in Oklahoma, presumably by the indirect effects of winter precipitation on seed productivity and insect density the following spring.

Geographic differences existed between the relationships we tested in this study. Longleaf pine masting sites were unevenly distributed throughout the specie's range where three states had one mast site from which to infer regional cone crop. Conversely, Florida had four masting sites that all reside within one climate division (Figure 4.1). Evidence for

oversampling in the Florida panhandle is seen throughout our analysis where Apalachicola, Tall Timbers, Blackwater, Eglin, and neighboring Escambia all share common counties where disease data were collected. Thus, this area might overestimate a region-wide effect in the combined analysis by resampling disease data and improving the overall relationship between the variables tested. Mast from the four of the five Florida sites are significantly correlated with one another (r = 0.47–0.89) with the exception being Tall Timbers that did not correlate with neighboring sites.

4.6 Conclusion

Longleaf pine masting research has principally focused on its interannual variability as it pertains to climate (Pederson *et al.* 1999; Leduc *et al.* 2015) and stand dynamics (Croker and Boyer 1975; Boyer 1979, 1990) and to our knowledge we are the first to examine its relationship to northern bobwhite quail and tick-borne disease incidence in humans. Northern bobwhite quail habitat preservation has inadvertently improved longleaf pine forests via prescribed burning (Van Lear *et al.* 2005) and the relationships explored herein can be integrated into wildlife and disease-vector management. Samish and Rehacek's (1999) review of pathogens and predators of ticks lists ground-foraging fowl such as the domesticated chicken (*Gallus domesticus* Linnaeus) and guinea fowl (*Numida meleagris* Linnaeus) that can significantly reduce tick populations. Wild turkey (*Meleagris gallopavo* Linnaeus), another ground forager found in longleaf pine forests, are known to consume immature blacklegged ticks while grooming and may be an effective biological control agent (Ostfeld and Lewis 1999). Here our results suggest the possibility of a similar effect from northern bobwhite quail if their tick consumption is sufficient to impact tick-borne diseases.

Several potential caveats exist that require elaboration. First, there is no definitive evidence for the spatial extent for masting within the native longleaf pine range. Mast counts for a particular cone location at best represent that of the state or region of collection. Fortunately, results from Guo *et al.* (2016) show that longleaf pine mast from sites closest together are highly correlated, providing evidence for a broad spatial footprint during masting years. Second, Brockway (2015) notes the spatial variation in longleaf pine stand quality and density and the annual reports are intended as a guide for the overall status of longleaf pine cone production as 97% of longleaf pine forests in its range are decimated and only a fraction of what remains is in good quality (Oswalt *et al.* 2012). As a result, we do not have any estimate on the variation in density of longleaf pine forests in our analysis or the variability of forest conditions across its range. That said there is a concerted effort from the Natural Resources Conservation Service (NRCS) to restore, protect, and enhance 4.6 million acres of former longleaf pine ecosystems by 2025, doubling the current extent of as of 2017 to 8 million acres (NRCS 2011). Third, our data are from a variety of sources with different scales used in our analysis that include mast site, county, climate division, and state. Our methods for correlating point (mast data) with areal (county cluster) data follow methodology used widely in dendroclimatology where tree data are aggregated to a site and correlated with climate-division data. Further, the use of multiple scales of data for analysis may be problematic yet were necessary for continuity of analysis across our study region spanning greater than 1,500 km. Last, these results should be treated cautiously as additional analyses are needed to support the viability of a longleaf pine mast/tick-borne disease relationship.

Figure 4.2. Diagram Showing The Influence Of Longleaf Pine Mast Of A Given Year That Can Positively Influence Northern Bobwhite Quail Populations The Year Following, Which In Turn Consume Ticks And Lower The Rate Of Tick-Borne Disease Incidence That Same Year As Reported By The CDC.

Our results provide baseline evidence for a possible connection (Figure 4.2) between longleaf pine mast and tick-borne diseases, particularly SFRG, that could help in the development of predictive models of annual tick-borne disease probability in the southeastern U.S.. Our results are based on correlative analysis, yet they provide insight into forest ecological connections lacking in the longleaf pine mast literature. If operative, the benefits of managing longleaf pine forest for northern bobwhite quail populations may have a twofold benefit by improving forest quality and lowering the incidence rates for tick-borne diseases in humans.

CHAPTER V

CONCLUSIONS

This dissertation examined longleaf pine cones from tree-ring and disease-ecology perspectives. All research herein used annual cone data provided by the USFS at the stand and individual-tree level. The cone crop data are publically available at the stand level and are based on averages obtained from at least 10 trees per site. These data are useful for anticipating large cone crops so that management practices could be initiated to promote successful regeneration. While useful for forest management, stand-level averages reveal nothing about cone-production variability between trees within a forest. When I was granted access to individual tree data through Dr. Dale Brockway of the USFS, I discovered how much intrasite variability exists between trees growing in close proximity. I learned that cone production was not equitable amongst trees, which is problematic when working with stand-level averages. Furthermore, interpreting longleaf pine as a masting species may conflict contemporary definitions that describe masting as a population phenomenon. This classification may be true at the stand-level of observation, or perhaps for bumper years, but likely not for all years. In the future I wish to examine how intrasite variability exists at all USFS masting sites, and the degree that each tree increases cone production during masting events.

Due to the interannual and intrasite variability of cone production there is not a strong influence that masting plays on influencing longleaf pine radial growth. While mast is

detectible through correlative analysis, I have showed that it has a minor influence on tree-ring based applications such as linear models that predict climate data. I examined whether a "whole tree" approach that paired annual radial growth with cone production would be useful and found that ring-width alone explained nearly all variation in PDSI in these models. This finding is useful for ascribing confirmation to a tree-ring based reconstruction using longleaf pine as it appears masting would not radically change or improve how these models accurately predict climatic data. One idea I did not examine was testing how much ring widths change during years where a strong drought and a masting event overlap. Perhaps only then could ring widths be affected, but as these events are rare their occurrence may only exist a few times in the cone-crop record. Furthermore, due to the limited masting dataset my models only examined masting and climate ~1968 to present. A future study could examine periods of masting and climate extremes for longleaf pine once these datasets develop over the coming decades.

My examination of the relationship between longleaf pine mast and tick-borne diseases should serve as a starting point for further investigations that examine the linkages between longleaf pine cones, climate, fire, seed predators, ticks, and human cases of tick-borne diseases. I acknowledge the many shortcomings of this research, yet there are encouraging results from this crude, range-wide analysis. I believe it is not unreasonable that longleaf pine seed predator populations would fluctuate with annual mast, especially during bumper masting years. I described how quail populations could spike due to large cone crops and these larger populations may have the ability to reduce tick populations. The next logical phase of this research would be to examine tick populations in masting stands.

Perhaps a future study could examine seed predation and whether these organisms also affect tick populations. Research exists that suggests fire ants (*Solenopsis saevissima richteri* Forel) can exclude tick and rodent populations in grasslands similar to longleaf savannas (Castellanos *et al.* 2016). Ants can also consume longleaf seeds, however seed predation by ants is low accounting for less than 10% of seed loss (Boyer 1963). It may also be advisable to examine how ant populations in cone-count sites also vary with masting cycles to see if they fit within the 'pine-cone' connection.

I hope results from this dissertation are useful toward a larger concerted effort to reforesting longleaf pine forests. I have inadvertently confirmed previous research regarding the benefits of reducing stocking density for improving longleaf pine mast. This was shown for the North Carolina cone-count site which led how I examined my data for that chapter. Additionally, I have revealed how variable longleaf pine mast is within a site. Hopefully as these datasets develop a better understand could be derived for how to manage forests for above average cone producers. Besides my agenda for supporting research in the longleaf pine community, I believe I have exposed ideas for how mast can be integrated with tree-ring data when used for climate analysis. While these data are a minor contribution to an overall "whole-tree" growth metric for longleaf pine, I believe it is useful to consider how masting in all tree species could influence tree rings beyond perturbations in climate. I hope that approaches like those I have shown continue to develop and improve the methods used in dendrochronology.

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